Specimen

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Horticultural Research is a journal for the publication of research papers and research reviews on subjects connected with horticultural plants or practices. Within this general context the Editors welcome offers of contributions in the fields of experimental agronomy, soil science, genetics, plant breeding, plant pathology and related subjects.

Practical reports on such subjects as performance trials of plant varieties and stocks will also be considered for publication provided that they are of more than local or routine interest. A section is available also for items submitted as short notes or comments. Books are accepted for review.

(*continued on p. 3 of cover*)

FOREWORD

By Professor J. H. Burnett, M.A., D.Phil., F.R.S.E.
Chairman of the Governing Body of the Scottish Horticultural Research Institute

The significance of horticultural research for the mental stimulation and bodily well-being of mankind increases daily. Since 1945 both the range and tempo of scientific work on horticultural problems has expanded in Britain and elsewhere. New centres of research, such as the Scottish Horticultural Research Institute, have been established; existing centres have been enlarged. Investigations have prospered and the information so gained is of immense potential value both to pure and applied biology and to innumerable growers. Yet many of us on the Governing Body became increasingly disquieted to see how the shortage of existing journals concerned with scientific horticulture set an unnatural restriction on publication. We were not surprised to learn that such restrictions extended far beyond Mylnefield. The matter was serious for, as Professor C. D. Darlington has put it (in another context), 'Discoveries unpublished are discoveries wasted'. It was a matter of real pleasure and relief therefore, to learn from Dr. Swarbrick that it was intended to launch a new publication in this field.

As I write this I have before me the proofs of the first number and information concerning future contributions. I am impressed both by the format and the contents and, naturally, I am particularly pleased that this venture has such strong associations with Scotland and, in particular, with Mylnefield. However, I know that the Editors and sponsors will not be satisfied unless this journal rapidly acquires an international flavour. I am sure they are right. I am equally sure that all horticultural scientists will wish to join me in congratulating Dr. Wood and Professor Fletcher on their enterprise and to wish them and the journal every success. I commend *Horticultural Research* to all interested scientists throughout the world both as a source of information and as a medium for their own publications.

University of Durham,
King's College,
Newcastle-upon-Tyne.

J. H. Burnett.

October, 1961.

EDITORIAL

The idea of introducing a new journal in Scotland to serve the needs of research workers in horticulture is not an entirely recent one. It was first considered at the time of the founding of the Scottish Horticultural Research Institute, about ten years ago, when it was foreseen that the work of the new station, together with that of similar centres then about to be established elsewhere in the United Kingdom, would probably lead to a substantially increased output in Britain of research papers concerned primarily with horticultural subjects. A considerable expansion of this kind has since taken place.

Although the Scottish Horticultural Research Institute, mainly for geographical reasons, has taken a special interest in the introduction of a new medium of publication in this field, it has at no time been the intention that a research journal published in Scotland should serve the Institute exclusively. Some regret is therefore felt that the five papers which form the main contents of the first number of *Horticultural Research* are contributed almost entirely from Mylnefield: but by proceeding in this way with the first suitable material to become available, we have been able to fulfil the aim of introducing Volume I during the present calendar year and within a short time of announcing the publication of the journal. Although *Horticultural Research* will doubtless continue to contain an appreciable number of Scottish papers, it will be our aim to serve a wider field and we shall welcome offers of contributions from any other sources, at home or overseas. In particular, we hope that the journal will provide a further link between research interests in Scotland and in those countries whose conditions or problems are closely related to our own, and with some of which an active collaboration already exists: examples are our common interests with the countries of North America, Scandinavia and northern Europe in the field of fruit breeding, with Scandinavia and Europe in work on vegetable varieties and breeding, and with North America, Europe and several countries elsewhere in work on the viruses and virus diseases of horticultural crops.

We should like to thank all who have helped to make possible the publication of the first number of *Horticultural Research*.

C. A. Wood.
W. W. Fletcher.

Hort. Res., 1961. Vol. 1, pp. 3-24

Studies on the Cultivation of Raspberries

I. EFFECTS OF PLANTING DISTANCES AND OF THE WINTER TIPPING OF CANES

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Summary

Distances between rows of 5½, 7 and 8½ feet, spacings between stools within the rows of 2, 2½ and 3 feet and heights of winter tipping of the canes of generally 4, 4½ and 5 feet were tested in factorial combination with the raspberry varieties Malling Promise, Lloyd George and Norfolk Giant in a 7-year field experiment. Increase either of inter-row distance or of stool spacing produced an improvement in performance per stool, because of the growth or survival of more canes per stool and a higher fruit yield per cane, but this failed to balance the reduction in cane population per unit area caused by the wider separation of the stools. Extension of planting distances therefore resulted in smaller yields per acre. The effect of the inter-row distances on yield per acre exceeded that of the stool spacings.

Increase of tipping height within the range of heights tested produced large increases of yield. Harder (i.e. lower) tipping of the canes slightly delayed ripening.

The productivity of raspberries planted at practicable distances and maintained as permanent stools is approximately proportional to the number of fruiting canes present. The varieties used in this experiment reacted very similarly to the cultural treatments tested, although some minor interactions were recorded. Close planting resulted in some years in greater losses of canes and buds associated with infections by fungi, chiefly *Botrytis cinerea* and *Didymella applanata*.

Introduction

COMMERCIAL crop management frequently involves the use of cultural practices which are not standardized, and the effects of which on growth and yield are imperfectly known. Studies to evaluate cultural factors are therefore essential in most attempts to increase the efficiency of crop production. Such studies are complementary to the breeding of

[1] Formerly at East Malling Research Station, Maidstone, Kent.

improved varieties and, in crops like the raspberry, to the production and maintenance of disease-free planting stocks.

This paper introduces a series of studies, started at Mylnefield in 1951, on cultural factors concerned in commercial raspberry growing in the Dundee area of Scotland, including procedures in soil cultivation, planting, manuring, cane selection, training and fruit picking. Comparatively little experimental work has been published on these topics in raspberries, although much technical information of an advisory nature has appeared, especially in North America. Practical aspects of the growing of the crop have been studied in America by Johnston and Loree (1927), Lott (1931), Darrow and Waldo (1933), W. G. Brierley and his co-workers, and others, and in Britain there have been manurial and other soil management trials, notably at East Malling and Long Ashton Research Stations.

Commercial raspberry plantations in the Scottish counties of Angus, Perthshire and Fife in 1959 occupied nearly 8,000 acres. Cultural practice in the area is uniform in that the post-and-wire system of support is always used and the planted canes are formed into permanent, spaced stools; but in other respects, including distances and methods of planting, systems of soil cultivation and manuring, methods of wiring, the selection of new fruiting canes and the winter treatment of the tops of the canes, some latitude exists. These are factors which can hardly fail to influence performance, and their effects are measurable experimentally. Although it is impossible to visualize a standard, uniform system of raspberry-growing applicable everywhere, it should be possible by experiment to eliminate undesirable practices and to evaluate others so that growers can better apply them to their own conditions.

Such studies are inseparable from questions of cost, and the cost factor may be decisive in the choice of a cultural method or its level of application. The real cost of a practice, however, can be assessed only from a knowledge of its effect on crop performance, and the present experiments have therefore been designed primarily to measure effects of cultural treatments on cane growth and fruit production. Cost differences in raspberry growing, especially where materials are mainly involved, can often be calculated or estimated, but it may become necessary later in this work to take field costings for certain practices more largely involving time. This will require trials of simpler design.

The Mylnefield authors have been responsible for the initiation and general conduct of this series of studies and the third author (G.H.F.) for the designs of the earlier experiments and the statistical analyses of the data.

The Experiment

Planting distances were chosen as a first subject of study because it was suspected that the inter-row distances popular in commerce—usually about $5\frac{1}{2}$ ft.—were inadequate for the vigorous new raspberry varieties and stocks introduced after 1945. Tractor cultivation had made a wider separation of

rows more practicable, and it was thought that the provision of a greater root-run and the admission of more light to the basal parts of the canes might improve performance. It was therefore decided to compare inter-row distances of $5\frac{1}{2}$ ft., 7 ft. and $8\frac{1}{2}$ ft., in combination with stool spacings within the rows of 2 ft., $2\frac{1}{2}$ ft. and 3 ft., the latter representing the range of spacings then used in commercial practice. Three varieties contrasting in ripening seasons and growth habit—Malling Promise, Lloyd George and Norfolk Giant—were included in order to observe their interactions, if any, with the cultural factors under test. The trial at planting thus had three varieties, three stool spacings within rows and three distances between rows, and was a straightforward 3^3 factorial. As it would have been difficult to manage an experimental area in which inter-row distances were constantly changing, this factor was put into main plots, with varieties and stool spacings in sub-plots. The unit sub-plot was one row 20 yd. long, and there were six blocks. Allowing for guards and landways, the total experimental area was just over $1\frac{3}{4}$ acre.

Three heights of tipping of the new fruiting canes after tying-in in winter were added as further treatments after the second growing season, making the experiment a 3^4 factorial. It would not have been practicable to split the plots further for this factor, and it was therefore necessary to confound some interaction with blocks. Tipping height was introduced as a factor at sub-plot level and the interaction of all four factors was partially confounded, the particular components for confounding being chosen at random. The partial confounding of the four-factor interaction at the sub-plot level meant that part of the three-factor interaction of varieties, stool spacings and tipping heights occurred on main plots. These two interactions were put into error and the other three-factor interactions pooled for testing purposes; the statistical analysis was then straightforward.

In all these studies the recognized good practice of the district has been followed in matters of management unconnected with the treatments under test: but an exception in the present experiment was that the young stool canes (canes arising directly from the stools, as distinct from suckers growing from roots) available each winter were not reduced in number except for the removal of damaged, weak, badly misplaced or diseased canes. All other canes were tied in, which meant that the cane populations in the most vigorous years of the plantation were high by normal standards. This was done because it was found by the second year that the numbers of new canes present in autumn varied with the treatments: thinning to a uniform cane number per stool would have destroyed these effects.

Farmyard manure was applied at 20 tons per acre in the winters 1951-52 (a year after planting) and 1953-54, and at 15 tons in 1955-56. A compound fertiliser ($8 : 7\frac{1}{2} : 12$) was used each spring at rates (fixed empirically) which declined from 10 and 12 cwt. per acre in the first and second years to 5 cwt. in the sixth and seventh years. For even application all manures were applied in weighed amounts per sub-plot, and the dressings, as in commercial

practice, were placed in narrow bands along the sides of the rows. All the sub-plots thus received equal manurial dressings, similarly placed, but the more widely separated rows had access to more soil space for root spread.

Fruit yields were the main summer record. The fruit was picked into pails, usually at from 4- to 6-day intervals, and weighed on spring balances readable to one ounce. Records were taken in autumn and winter of the numbers of new canes available after 'stooling-up' and the proportions of them that reached the top wire and tipping heights after tying in. The top wires were set at 6 in. below the tipping levels. Routine hoeing and stooling-up in spring and summer, work which considerably influences the numbers and quality of new canes present in a plantation in autumn, was done in this and other experiments by experienced staff unfamiliar with the records that were to be taken.

It is possible to compare yields on the basis of crop per stool, per row or per acre. Each of these is adopted in some of the following text-figures, but the record of greatest practical importance is crop per acre, and it is on this that all statistical calculations are based. The use of split plots in the design meant that from the beginning the effects of distances between rows were less accurately compared than those of other treatments; but this was quite acceptable, as these effects must be very large to be important. The introduction of the factor of tipping heights, and consequent partial confounding of some interactions, had only a very small effect on the accuracy of the other comparisons, while ensuring that the main conclusions would be more broadly based.

Differential tipping treatments were first applied in 1953, when heights of 5, $4\frac{1}{2}$ and 4 ft. were compared. After the vigorous growth of that year the heights for 1954 were raised to $5\frac{1}{4}$, $4\frac{3}{4}$ and $4\frac{1}{4}$ ft., but this led to so much wind and picker damage in the highest-tipped rows that the heights for 1955 were reduced to the former levels. Drought in 1955 depressed growth, and in the following winter the Lloyd George rows were tipped throughout at 4 ft., the Malling Promise at $4\frac{1}{2}$, 4 and $3\frac{1}{2}$ ft. and the Norfolk Giant at 5, $4\frac{1}{2}$ and 4 ft. These changes, made on practical grounds, meant that an analysis of the general effect of tipping was possible only for the years 1953-55. For subsequent years all effects involving tipping height had to be examined within each variety separately. This in turn meant a rearrangement of the statistical analysis, with a special calculation of that part of the confounded interaction occurring on the main plot level. Tipping heights of $4\frac{1}{2}$, 4 and $3\frac{1}{2}$ ft. were applied to all three varieties in 1957, but the analysis still took account of the differential treatment of the varieties in the previous year.

Main Results

Main Effects of Planting Distances on Fruit Yields and Cane Populations

Fig. 1 shows the average accumulated yields per *sub-plot* (i.e. per row of 20 yd.) for the three inter-row distances over the whole period of the experi-

ment. The $8\frac{1}{2}$ ft. rows gave the highest total yield and the $5\frac{1}{2}$ ft. rows the lowest, but these differences were not clearly established until the fourth growing season. In the first two years the $5\frac{1}{2}$ ft. rows in fact cropped the best, probably because of better mutual shelter afforded by the canes at this

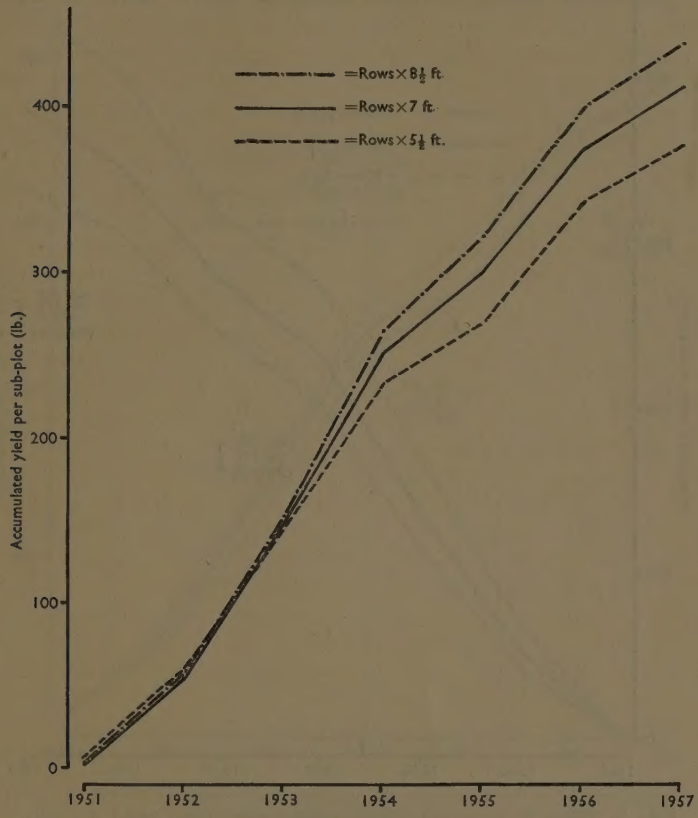

FIG. 1. Effect of inter-row distance on accumulated yield per sub-plot (3 varieties averaged).

distance. (This result has recently been repeated in the early years of another experiment, containing inter-row distances of 6 ft. and 8 ft.) After 1953, however, the wider rows were clearly superior in total yield, although by 1957 it appeared that the three treatments had ceased to diverge and were nearly equal in annual yield.

In Fig. 2, which gives the cropping at the three inter-row distances in yields *per acre*, the positions in Fig. 1 are reversed. Despite their higher yield per unit length of row, the $8\frac{1}{2}$ ft. rows were lowest in productivity per

acre, and conversely the $5\frac{1}{2}$ ft. rows were highest. The better performance per plant arising from wider separation of the rows thus failed to balance the loss from the reduction in plant population per unit area.

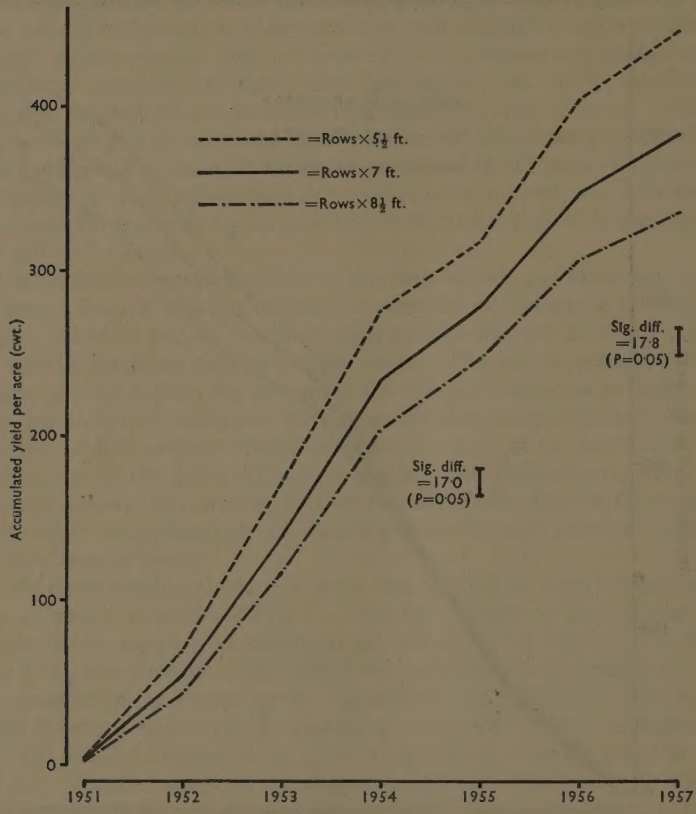

FIG. 2. Effect of inter-row distance on accumulated yield per acre (3 varieties averaged).

The effects of the three stool spacings on accumulated yield per acre are shown in Fig. 3. Like wider inter-row distances, wider spacings of the stools within the row enhanced the performance of the individual stools, but again this failed to balance the reduction of plant population. The sub-plots with stools spaced at 24 in. were therefore highest in yield. Because of the design of the experiment, changes in sub-plot yields due to stool spacings are directly reproduced on conversion of the data into yields per acre, and Fig. 3 can therefore be compared directly with both Fig. 1 and Fig. 2. Comparison with Fig. 1 shows that by 1957 the total cropping differences per sub-plot

associated with stool spacings, and in favour of close spacing, were little more than half the size of those caused by inter-row distances, which were in favour of the wider distances. Comparison with Fig. 2 shows that the effect of stool spacings on yield per acre was very much smaller than that of inter-row distances. These results are examined in more detail later.

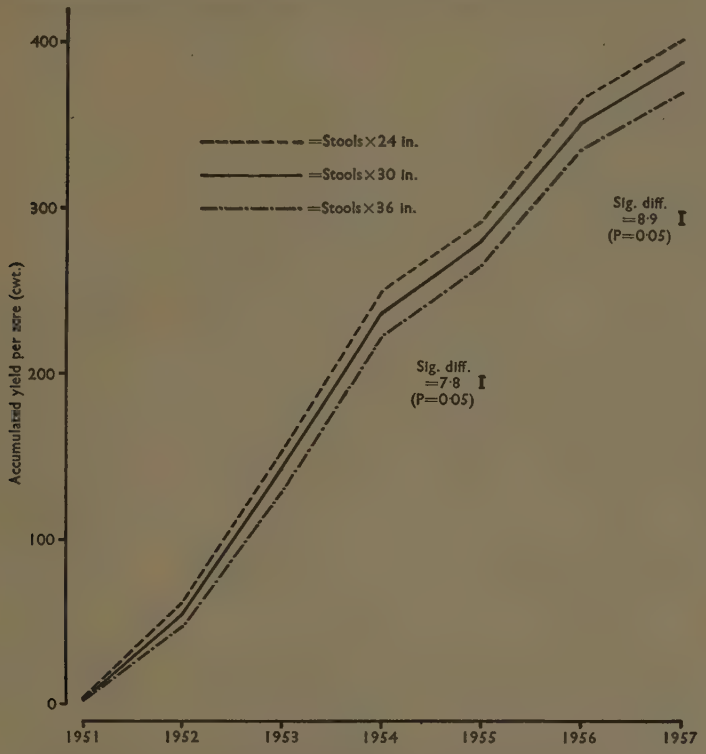

FIG. 3. Effect of inter-stool spacing on accumulated yield per acre (3 varieties averaged).

Lastly, Fig. 4 shows annual and accumulated yields per acre for all nine combinations of inter-row distance and stool spacing, averaged (as in the preceding graphs) for the three varieties. The closest planting distance ($5\frac{1}{2}$ ft. × 2 ft.) gave the highest total yield and the widest distance ($8\frac{1}{2}$ ft. × 3 ft.) the lowest, with the other combinations placed in regularly descending order. The total records show no overlapping of the yields of closely spaced rows with widely spaced stools by the yields of widely spaced rows with close stools, although this occurred occasionally in the first five seasons: for example, in 1951 and 1952 all three varieties cropped better at $8\frac{1}{2}$ ft. × 2 ft. than at 7 ft. × 3 ft. The advantage in plant population possessed

by the wider rows with closely spaced stools was countered in the long run by the fact that decrease of inter-row distance was more effective in raising yield per acre than decrease of stool spacing.

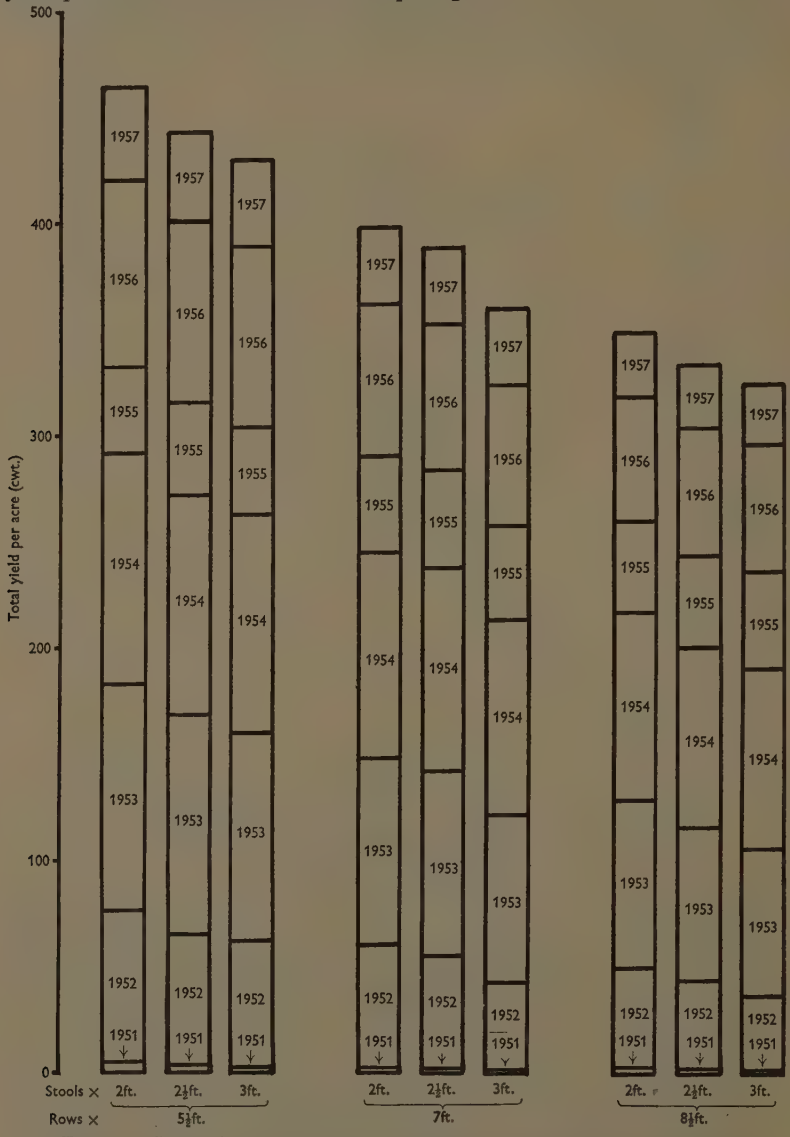

FIG. 4. Effects of combined inter-row distances and inter-stool spacings on yield per acre (3 varieties averaged).

Fig. 4 also gives a general picture of the annual variations in yield. Cropping at all planting distances rose to a peak in 1954, declined sharply in 1955 through drought and other causes (see below), rose again in 1956, when the quality of the fruiting canes was excellent, and fell in 1957 to near or below the 1955 levels. The rising output in the early years reflected the normal development of the plantation, with canes increasing each season in numbers and height.

The main results here given were confirmed by statistical analyses of the yields per acre. The combined 1951 and 1952 yields and the yields in 1953 showed very highly significant differences ($P < 0{\cdot}001$) associated with inter-row distances and stool spacings, but after 1953 the effects of stool spacings were not significant in individual years. Inter-row distances produced large differences of yield in 1954, 1956 and 1957 but no significant effect in 1955, when the advantage in numbers of plants per acre possessed by the closer rows was countered by their greater susceptibility to the dry conditions. Both inter-row distances and stool spacings produced very highly significant effects on the total crop for the whole period (1951-57), but those of stool spacings were largely residual from the 1951-53 period.

Fig. 5 shows the numbers of canes tied in for fruiting per sub-plot in the last five years of the experiment, averaged separately for inter-row distances and stool spacings. Also shown are the average yields of fruit. Relationships between cane populations and yield shown in this text-figure are examined in more detail below, but it is clear that the general effects of planting distances on the numbers of sound canes available for tying-in were similar to their effects on yield: that is to say, cane numbers per sub-plot rose as inter-row distances widened and as stool spacings decreased. It should be noted that the cane numbers shown for each year, recorded in late winter, represent both the growth of the preceding year and the cropping potential of the current season.

Statistical analyses for cane populations were made not on numbers of canes per sub-plot but on numbers per stool, which tended to rise as inter-row distances and stool spacings increased. The differences associated with stool spacings were very highly significant ($P < 0{\cdot}001$) in each of the years 1953-57. There were no differences associated with inter-row distances in 1953, but significant differences occurred at $P < 0{\cdot}01$ in 1954, at $P < 0{\cdot}001$ in 1955 and 1957 and at $P < 0{\cdot}05$ in 1956. Again because of the design of the experiment, the effects of inter-row distances on cane numbers per stool are directly reflected in the inter-row distance histograms shown in Fig. 5, whereas for stool spacings the differences shown in numbers per sub-plot are in the reverse direction from differences in numbers per stool. The additional stools present at the closer spacings more than made up for the reduction in cane complement per individual stool.

Relationships of Stool and Cane Populations to Yield

Although the effects of planting distances on cane populations resembled in general their effects on fruit yield, Fig. 5 also shows that the influence of

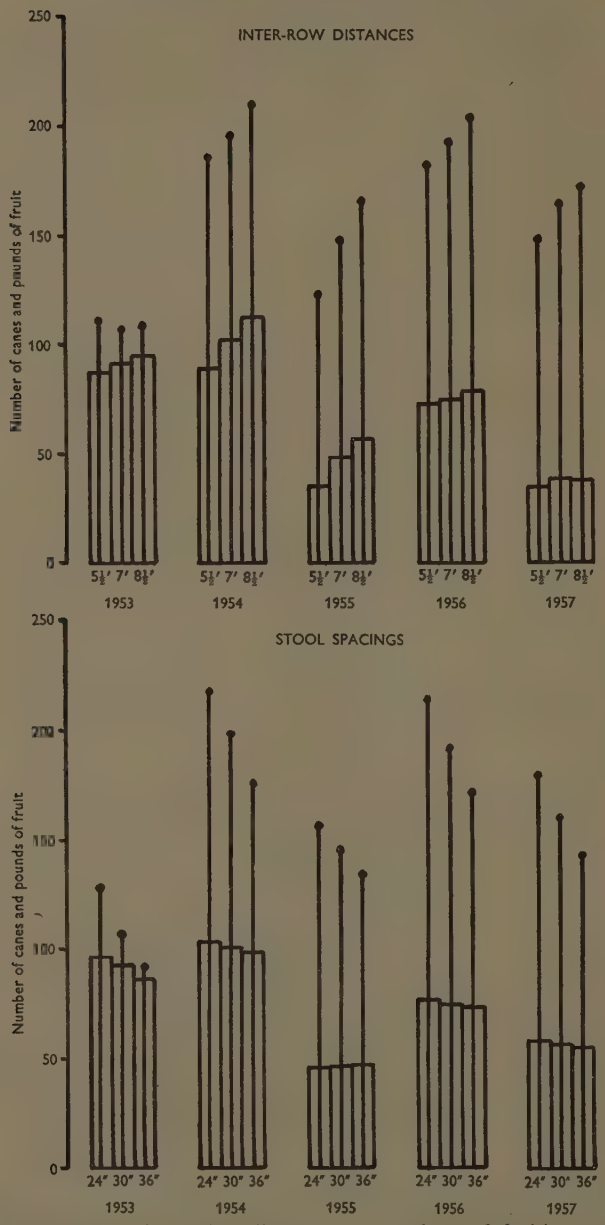

FIG. 5. Effects of planting distances on numbers of fruiting canes (vertical lines) and yields of fruit (blocks) per sub-plot (3 varieties averaged).

stool spacings on cane numbers per sub-plot was proportionately much greater than their influence on yield. This was because the canes, as they increased in numbers per length of row with closer stool spacings, fell in individual productivity. This occurred each year, but particularly in 1955 when the effects of drought and fungal infection were worst where the canes were most crowded. Inter-row distances, especially in 1954, 1955 and 1956, affected yields per sub-plot more nearly in proportion to their effects on cane numbers, showing that their influence on individual cane performance was small. Yields per cane in fact rose slightly in 1953, 1954 and 1955, and fell in 1956 and 1957, with increase of inter-row distance. The large effect of inter-row distances on cane numbers present in 1955 was probably due mainly to excessive losses of young canes by breakage and fungal diseases in the $5\frac{1}{2}$ ft. rows in the wet summer of 1954.

Fig. 5 shows further that yield per individual cane varied from year to year, irrespective of planting distance. Although the numbers of fruiting canes fluctuated irregularly, yields per cane in all three varieties declined fairly steadily between 1953 and 1957. Performance per cane was highest either in 1953 or in 1952 (when there were no cane records), and yields per row and per acre were highest in 1954, the fourth year of growth.

Because of the varying influence of seasonal factors on this experiment, some of the treatment effects can be demonstrated more clearly by calculations based on the total cane populations and fruit yields for the period 1953-57, the years for which complete records exist. Graphs prepared in this way are shown in Fig. 6. In these, the lowest value of every function plotted is equated with unity, and all higher values are expressed proportionately. Fig. 6a shows changes in the relative values of yield per cane, canes per stool and yield per stool, all of which increased with increasing planting distances. Yield per cane, however, was affected much more by stool spacings than by inter-row distances. Increase of stool spacing, by giving a combination of more canes per stool and a better performance per cane, produced a rapid rise in yield per stool. Fig. 6b shows graphs for canes and yields per sub-plot. Both of these increased with increase of inter-row distance and decrease of stool spacing, and therefore were of lowest value at the $5\frac{1}{2}$ ft. $\times$ 3 ft. planting distance. Stool numbers per sub-plot are also shown. The graphs for canes and yield illustrate that inter-row distances, with their small effect on individual cane performance, affected yields per sub-plot in close proportion to their effect on cane numbers. Although the effect of stool spacings on cane numbers per sub-plot was greater than that of inter-row distances, their effect on sub-plot yields was smaller, because closer stool spacing depressed individual cane performance.

Notwithstanding these detailed effects, yields per sub-plot were roughly proportional to the numbers of canes present, from which it follows—as shown in Fig. 6c—that yields and cane populations per acre were also fairly closely correlated. Although with progressively closer planting the graphs for cane numbers and yield diverge, owing to declining performance per

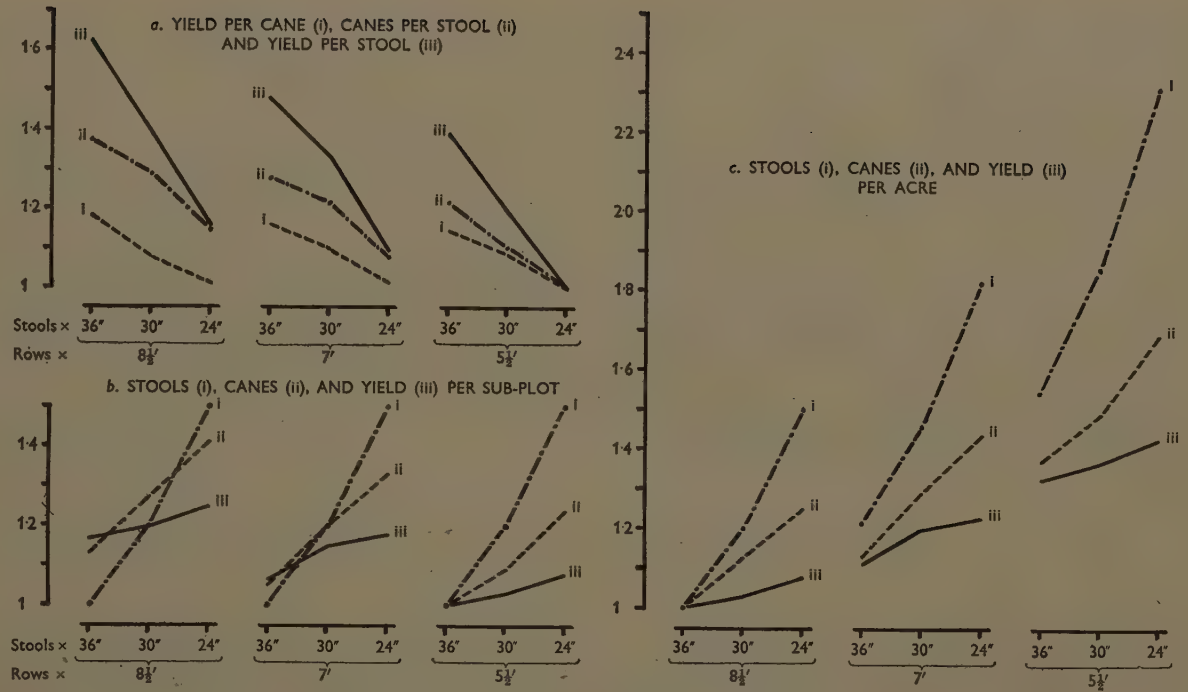
a. YIELD PER CANE (i), CANES PER STOOL (ii) AND YIELD PER STOOL (iii)
b. STOOLS (i), CANES (ii), AND YIELD (iii) PER SUB-PLOT
c. STOOLS (i), CANES (ii), AND YIELD (iii) PER ACRE
Stools ×
Rows ×
36″ 30″ 24″
8½′ 7′ 5½′

FIG. 6. Relationships between numbers of stools, total numbers of fruiting canes and total fruit yields, for the period 1953-57 (3 varieties averaged). Ordinate scales are proportional. Lowest value of each function = 1.

cane, it is clear that yield is more closely related to populations of canes than of stools. It may be related still more closely to populations of productive fruiting laterals.

Main Effects of Tipping

Raspberry canes are normally winter-tipped at from 6 in. to 8 in. above the top supporting wire, which is positioned according to the general height and vigour of the growth. In Scotland the height above ground at which canes are tipped in mature, well grown plantations is about 5 or $5\frac{1}{4}$ ft., roughly the highest level that allows pickers to reach the topmost fruit without breaking the laterals.

Over the period 1953-55 the raising of tipping height from the lowest to the highest level gave total crop increases (averaged for planting distances)

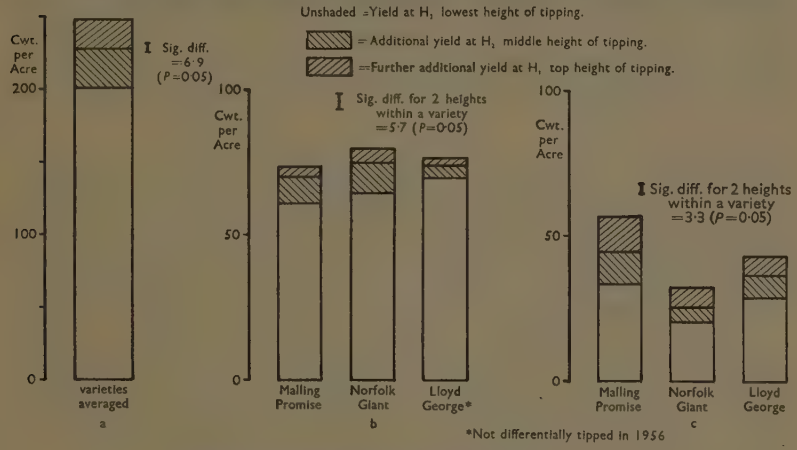

FIG. 7. Effects of tipping height on yield per acre. a, 1953-55; b, 1956; c, 1957.

exceeding $2\frac{1}{2}$ tons per acre in Norfolk Giant and Lloyd George and 3 tons in Malling Promise. The differences, both in individual varieties at each inter-row distance and in average yields for all varieties and planting distances (Fig. 7a), were very highly significant ($P < 0{\cdot}001$). There were no significant interactions of varieties with tipping heights (see below). Figs. 7b and 7c give the 1956 and 1957 results. In 1956 the hardest-tipped sub-plots of Norfolk Giant and Malling Promise were significantly lowest in yield, but in Lloyd George also, the variety not differentially tipped that year, the rows previously tipped hardest yielded significantly less than those previously most lightly tipped. This was not caused by differences in the proportions of canes reaching the standard tipping height of 4 ft. (p. 18). In 1957 lighter tipping again gave large increases of yield in all three varieties, but especially in Malling Promise.

The main reason for these results, which are in general agreement with those of Lott (1931), Brierley (1931) and Johnston and Loree (1927) in America, was clearly the extra length of cane fruited when tipping heights were raised. In many varieties—typically in Malling Promise, perhaps least in Lloyd George—the region of the cane normally severed at tipping produces some of the best laterals. There could, however, conceivably be other contributory factors, such as effects of tipping on the numbers of new canes available in autumn and on the proportions of these attaining given heights. As shown later, effects on height could not be established. As for numbers, an examination of the cane records for the winters from 1953-54 to 1956-57 yielded no consistent evidence that the preceding years' tipping treatments had influenced the numbers of new canes available. In Norfolk Giant there was a tendency each year for the numbers to decrease with harder tipping (due perhaps to greater losses through wind exposure), and in 1955-56 the hardest-tipped rows had significantly fewer canes ($P < 0{\cdot}05$) than the others: but Malling Promise in 1954-55 and 1955-56 showed the reverse tendency, the canes on the lightest-tipped rows in 1955-56 being significantly fewest.

Treatment Interactions affecting Cane Populations and Yields

The interactions between varieties and cultural treatments in this experiment were small in comparison with the main effects, and not all of them were consistent. From this it follows that the cultural factors tested affected the three varieties fairly equally, and that the present results may well apply to red raspberries in general.

The most frequent interaction affecting fruit yields was between varieties and inter-row distances, and showed that the proportional rise in yield per acre as these distances decreased was greatest in Lloyd George and least in Norfolk Giant. For reasons given, this means that the fall in individual plant performance as inter-row distances decreased was least in Lloyd George and greatest in Norfolk Giant. This interaction was significant at the 1 per cent. level in the combined 1951 and 1952 yields and at the 5 per cent. level in 1954, and was strongly evident ($P < 0{\cdot}001$) in 1957 and in the total yields for 1951-57 (Fig. 8). The natural ability of Lloyd George to form productive fruiting laterals almost down to ground level, where shading is greatest, seems to offer the simplest explanation of its adaptability to narrow inter-row distances.

The 1953-54 and 1954-55 winter records of percentages of canes reaching prescribed tipping heights showed interactions reflecting known differences in growth height between the three varieties, Norfolk Giant being tallest and Lloyd George shortest. The cropping data showed a general tendency for the advantage (in terms of percentage increase of yield per acre) of raising the height of tipping by 1 ft. to be least in the $8\frac{1}{2}$ ft. rows and greatest in the $5\frac{1}{2}$ ft. rows. This effect was most marked in 1954 and, for Malling Promise, in 1957. It was not clearly seen every year and did not appear in the drought

year of 1955; but the total crop for the seven years of the trial showed, despite all the changes in tipping heights, that the effect of higher tipping increased steadily as the distance between rows decreased.

As might have been expected, there was less evidence of inter-relationship

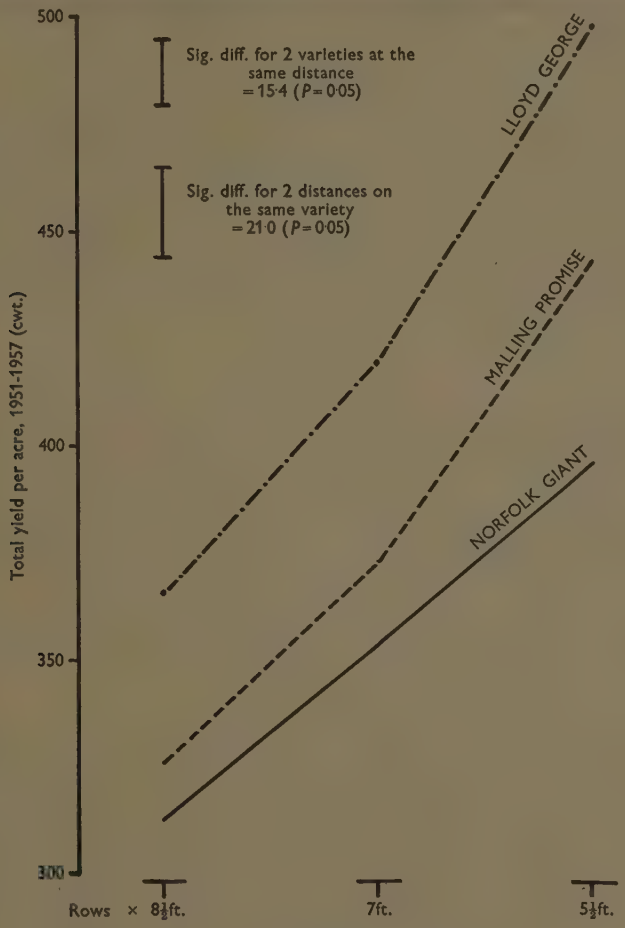

FIG. 8. Effect of inter-row distance on the total yields per acre of the three varieties.

of tipping height with stool spacings. The 1957 data for Malling Promise and the 1956 data for Norfolk Giant suggested that the benefit of higher tipping was diminished at the widest (36 in.) spacing, whereas the 1957 data for Lloyd George suggested the reverse. There were no indications of effects on the total crop.

Although there were no significant interactions between varieties and tipping heights, the smallest increase of yield from higher tipping over the whole period of the experiment was in Lloyd George. This accords with the frequently observed fact (at least in Scotland) that the top parts of Lloyd George canes more than four or five feet high tend to be thin and of poor quality, whereas canes of some other varieties are strong and productive at this level.

It was not possible to relate interactions in the cropping data of any particular year to interactions in the cane growth records of the previous winter, an indication that the growth records were not closely enough related to yield to reflect minor effects. This is not surprising in view of the simple growth records mainly used and the seasonal and other factors that influence cane quality and performance. Since, however, the crop records of the experiment were very carefully taken, the interactions which they show can probably be accorded considerable weight even if they are not fully explained in terms of growth.

Minor Results

Cane Length

If canes differ in fruiting performance, it should be possible to relate the differences to variation in such characters as length, percentages of nodes producing fruiting laterals and the number, type and individual productivity of laterals (Wood and Robertson, 1957). It was impracticable in this experiment to measure the length of the canes before tipping, but for four winters the proportions of canes reaching the prescribed heights of tipping were recorded on all sub-plots, and these records were used as an indication of differences in average height. On this limited basis the only large and consistent differences were between varieties. Neither inter-row distances nor stool spacings produced significant effects.

Actual records of cane heights before tipping might have shown some effects of the tipping treatments themselves on the amount of new growth, for MacDaniels (1922) stated that new growth in the variety Herbert was greatly stimulated by severe pruning of the fruiting canes late in the previous winter. The only opportunity to look for such effects in this experiment occurred in the winter 1955-56, when all the sub-plots of Lloyd George were tipped at 4 ft; but the percentages of canes reaching this height showed no effects of previous tipping.

Cane Health and the Formation of Fruiting Laterals

It is well known that raspberry canes vary in the numbers of fruiting laterals they produce, particularly near ground level, and it was thought that any cropping advantage arising from wider planting might be associated with a greater development of laterals in this zone, perhaps because of better light penetration.

Unfortunately, differences of bud performance which might be caused in healthy plants by purely physiological factors, such as variations in light or moisture supply, are difficult to separate in the field from effects of diseases, particularly of the fungal diseases spur blight (*Didymella applanata*) and grey mould (*Botrytis cinerea*). These are present to some extent in most plantations and often become serious in wet seasons, causing damage or death to buds and canes. Infection might be expected to increase with closer planting. In experiments of the present kind the field observer has to record the behaviour of buds and laterals and try to decide, from climatic conditions and other evidence, how far the effects seen are due directly to physiological factors and how far they arise indirectly from effects of the experimental treatments on disease incidence.

Records of this kind were first taken in 1955, following the wet summer and autumn of 1954 when *Botrytis* had been very prevalent. In 1955 the rows of Norfolk Giant and Malling Promise contained many dead or partly dead canes, most of them bearing sclerotia of *Botrytis* and pycnidia of *Didymella*. In inland parts of east-central Scotland in the same year there was a high incidence of cane death, mostly in Malling Promise, which circumstantial evidence suggested had been caused by late winter frosts (Wood and Robertson, 1957); but this factor had not operated seriously at Mylnefield. There the losses were heaviest in the present experiment, which was on a more frost-protected site than others but where the canes were overcrowded.

Table I shows that percentages of dead canes (including canes dead above the lower wire) and numbers of nodes with dead buds on live canes both

TABLE I

Percentages of dead canes per sub-plot and, in brackets, average numbers of dead-budded nodes per live cane (June 1955)

Variety	*Inter-row Distance*			*Stool Spacing*		
	5½ ft.	7 ft.	8½ ft.	24 in.	30 in.	36 in.
Norfolk Giant	44·74 (4·05)	30·35 (3·38)	25·93 (3·15)	38·35 (3·62)	31·62 (3·46)	31·05 (3·50)
Malling Promise	22·96 (1·99)	17·33 (2·20)	14·95 (1·90)	18·82 (2·07)	20·17 (2·01)	16·31 (2·02)
Lloyd George	9·91 (1·53)	5·39 (1·38)	4·72 (1·35)	7·96 (1·55)	7·25 (1·42)	4·80 (1·30)
Varieties Averaged	25·87 (2·53)	17·69 (2·32)	15·20 (2·13)	21·71 (2·41)	19·68 (2·30)	17·39 (2·27)

increased as distances of planting became closer. The effect on the percentage of dead canes was very marked both for inter-row distances ($P < 0{\cdot}001$) and stool spacings ($P < 0{\cdot}01$), but neither factor had a significant effect on the numbers of dead-budded nodes. These losses of canes, substantial in

Norfolk Giant and Malling Promise, must have contributed to the fall in fruit yields in 1955, and reductions in cane performance in the directions indicated are compatible with the records in Fig. 5. It appears, therefore, that under certain seasonal conditions close planting can lead to increased cane losses associated with the presence of fungal diseases; but the losses in this experiment may have been unusually high because the canes were not thinned.

Fruiting laterals were recorded in 1956 and 1957 alone, and only on the parts of the canes below the bottom wire (27 in. above ground), where any effect of planting distance was expected to be greatest. Nodes in this zone were first counted on the ten middle stools of each sub-plot, and later a record was taken of the percentages of counted nodes that produced fruit-bearing laterals. Rosette-like laterals and other short flowerless growths were excluded. The results showed no clear effects of inter-row distances; but in 1956 the 36 in. stool spacing gave a significantly higher percentage of cropping nodes than either of the other spacings, and in 1957 it gave a significantly higher percentage than the 30-in. spacing (Table II). There were also marked differences in lateral formation between the two years, and large differences (not shown in the table) between the varieties, Malling Promise having the fewest laterals and Lloyd George the most.

TABLE II

Percentages of nodes, below the bottom wire, forming laterals contributing to the crop (3 varieties averaged)

Year	*Stool spacing*			*Sig. diff.*
	24 in.	30 in.	36 in.	($P=0{\cdot}05$)
1956	43·7	43·4	45·9	2·1
1957	33·1	31·6	33·8	1·7

The fruiting canes in 1956 were very sound and healthy, having grown in sunny, dry conditions in 1955, whereas the 1957 canes showed much fungal infection of the kind described above. The figures for the two years reflect this difference. It is impossible to say to what extent the small differences associated with stool spacings were due to different intensities of competition affecting the functioning of healthy buds or to differences in the incidence of fungal infection. Since the figures in Table II refer to the lower parts of the canes only, and discount healthy flowerless laterals, they cannot be compared with the figures for dead-budded nodes in Table I.

The 1956 records of percentages of nodes forming cropping laterals below the bottom wire showed no effects of the tipping treatments, but in 1957 the lightest-tipped rows of Lloyd George had a significantly higher percentage of productive nodes than the hardest-tipped ($P<0{\cdot}05$). This isolated result was contrary to those of Brierley (1934) for the variety Latham,

on which tipping heights of 5 ft., 3 ft. and 1¼ ft. were compared. There was again no effect in Malling Promise or Norfolk Giant.

Fruit Quality and Times of Ripening

Distances of planting and heights of tipping might be expected to influence raspberry fruit quality mainly by affecting plantation density and hygiene. Large differences of tipping height might also affect size. It was impracticable in this experiment to grade the crops for size, ripeness or degree of mould infection, but the impression was gained that weather conditions and success in keeping abreast of picking were more important determinants of quality than the cultural treatments tested. On several occasions when weather delayed picking there was a general development of grey mould throughout the experiment. In 1953 the disease affected the unripe fruit, causing unavoidable loss, but again its incidence seemed fairly uniform. In most years, however, maintenance of quality was largely a matter of timely picking to avoid the development of mould on the ripe fruit. The sub-plots of any one variety were all picked an equal number of times, and, except for interruptions by weather, on the same dates. In the dry season of 1955, when much of the fruit was small, that from the 5½ ft. rows was the poorest.

The records from 1954 to 1957 were examined for possible treatment effects on times of ripening, by calculating the percentages of total crop harvested by each picking date. Any effects of planting distances were very slight. There were indications in Lloyd George in 1954, in all three varieties in 1956 and in Lloyd George and Malling Promise in 1957 that close proximity between rows gave slightly earlier ripening: but in 1955 there was apparently no effect of planting distances on the ripening of Lloyd George or Malling Promise, while the later variety Norfolk Giant tended to ripen more readily as the rows became wider apart, perhaps because the widely spaced rows suffered less from the drought. Even allowing for the fact that the experiment was normally picked completely on each date, which would tend to mask differences in ripening times, it is clear that the seasons of the varieties were not materially affected by the planting distances.

TABLE III

Percentages of total crop harvested by each picking date at three levels of winter cane-tipping. (H_1, H_2 *and* H_3=*light, medium and hard tipping*)

(i) *Norfolk Giant in* 1954				(ii) *Malling Promise in* 1957			
Date	H_1	H_2	H_3	*Date*	H_1	H_2	H_3
28–29/7	5·9	4·0	2·3	3/7	11·1	8·2	4·9
2–3/8	20·9	17·4	12·9	8/7	40·1	34·4	25·1
9–11/8	56·4	56·2	51·9	11/7	52·1	47·5	38·6
15/8	81·6	81·1	79·7	16/7	77·0	73·5	66·7
20/8	89·6	89·4	88·5	22/7	90·1	87·1	82·3
24/8	96·7	96·4	96·2	26/7	95·4	92·8	90·1
30/8	100	100	100	31/7	98·5	97·3	96·4
				6/8	100	100	100

Similar calculations applied to yields at the different tipping heights showed that harder tipping usually delayed ripening. This was true for Norfolk Giant and Malling Promise in all four years and for Lloyd George in 1957: it occurred slightly in Lloyd George in 1954 but not in 1955, and this variety was not differentially tipped in 1956. Typical examples of the effect, which was always small, are shown in Table III. The tendency for hard tipping to delay ripening has been noted in America (Slate, Braun and Mundinger, 1953) and is known in garden practice.

Conclusions

These results show that where yield per unit area is the primary consideration and the stool system of culture is used, raspberries should be planted at the closest distances consistent with efficient cultivation and management. Wide planting distances adopted with the aim of improving plant performance, or because land is plentiful, will lead to reduced yields per unit area, because the improvement in individual plant performance will fail to balance the reduction in cane population. Yield in stooled raspberries grown at practicable planting distances is related fairly closely to the numbers of canes fruiting, and probably still more closely to the numbers of fruit-bearing laterals. In showing that yield is thus correlated with the population of productive units per given area, the present results agree with those reported for many other crops. (The behaviour of raspberries grown as continuous rows of non-stooled canes will be discussed in a later paper.)

The results of the winter tipping treatments were very clear, and fully justify the practice of tipping canes as high as possible when growing for maximum yield. Height of tipping is limited generally by the ability of pickers to reach the topmost fruit without breaking the laterals, and sometimes by the exposure of plantations to wind.

The difference in total yield between the closest and widest planting distances, averaged for the varieties, was 139 cwt. per acre over six cropping seasons, or an average of more than a ton a year. It is very doubtful if a cropping difference even approaching this size could be established between different grades of health-certified nursery stock of a single variety grown under uniform treatment, and correct planting distances are therefore essential if the full potentialities of healthy stocks are to be realized. The results also emphasize the need for standardized planting methods in trials to compare varieties and stocks.

This experiment was concerned solely with plant and plantation performance, and does not show whether the yield of closely-planted raspberries justifies their higher costs of cultivation. Inter-row distances of $5\frac{3}{4}$ ft. and 6 ft., however, are in general use in eastern Scotland, and standard equipment exists to handle them. The largest single cost in raspberry growing is that of picking, and where this is done by piece-work, on a weight basis, it must

be to the grower's advantage to produce the maximum crop per unit area compatible with efficient management before and during picking. Fig. 6c suggests that inter-row distances of less than 5½ ft. would give still higher yields, but such close rows planted with any but the most erect-growing varieties would be very difficult to manage on a field scale.

The effects on the raspberry stool of close planting are to depress both the number of sound new canes produced (or surviving by the end of the year) and the fruiting performance of the individual cane. These effects are exerted more strongly by stool spacings within the row, where the plants are closest together, than by inter-row distances: but the influence of stool spacings on yield per unit area is fairly small (Fig. 3), because the loss in individual plant performance at close spacings is roughly balanced—in this experiment, a little more than balanced—by the increase in the number of plants per length of row. Distances between rows, within the range practicable for cultivation, have a much greater effect on yield per unit area (Fig. 2), since they produce large changes in plant populations without greatly affecting individual plant performance. Increased failure of canes and possibly of buds, associated with but not necessarily wholly caused by fungal infections, was a factor reducing cane efficiency at close planting distances in some years of the present experiment (Tables I and II). It is doubtful if the treatments affected the percentages of new canes which reached the prescribed tipping heights, and there was no clear effect of tipping height on the formation of laterals on the lower parts of canes. In general, the effects of planting distances on individual plant performance resembled those reported by Hodgson and Blackman (1956) for the field bean (*Vicia faba*), but the plant densities studied by these workers were of wider range, and the effects more extreme.

Since the main results of this study were so clear, it seems reasonable to regard them as of general application where raspberries are grown. In areas where the crop ripens more quickly than in Scotland the risk of loss from grey mould at close planting distances may be greater, but perhaps still a serious hazard only in exceptional years.

Acknowledgments

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CHEMICAL CONTROL OF OVERWINTERED ANNUAL WEEDS IN A RASPBERRY PLANTATION

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SUMMARY

Herbicides were applied to the overwintered annual weed flora present in a seven-year-old raspberry plantation on dates in February, March and May 1959. There had been no cultivations since the previous summer, and none took place after application of the treatments. Of twenty-one treatments tested, only three—2·0 lb. simazine, 4·0 lb. monuron and a mixture of 3 gal. phenols with 4·05 lb. fenuron[2]—gave adequate weed control for six months without apparent crop injury. Other treatments which controlled or checked existing weeds either did so at the expense of damage to the crop or showed no residual activity against germinating seedling weeds.

INTRODUCTION

BETWEEN the times of fruit picking in summer and tying-in of new canes in winter, the cultivation of raspberry plantations for weed control is normally impracticable. Under traditional systems of management weeds grow freely during this period, and, unless the winter is unusually severe, a well-established growth of annual weeds survives into the spring. In some areas creeping buttercup (*Ranunculus repens*) is also a notable overwintering species (Robinson, 1960). It is common practice in Scotland to rely upon checking such weed growth with the tar oil spray which is usually applied in late winter as a control for raspberry moth larvae, but this treatment seldom achieves more than a severe scorching of the hardier weeds, like *Poa annua*, which soon resume active growth. The present experiment was an attempt to achieve the complete destruction of a carpet of overwintered weeds by chemical means alone, and thereby to avoid the damage that may occur to the roots and young emerging canes of the crop from mechanical cultivations conducted in late winter or spring. The materials used were chosen largely on the basis of previous work in raspberry cane nurseries (Wood and Sutherland, 1960) but included a number of experimental compounds and mixtures specially supplied by manufacturers.

[1] Present address: The North of Scotland College of Agriculture (North Region), Drummondhill, Stratherrick Road, Inverness.

[2] Rates of application of herbicides are quoted in this paper in pounds or gallons of active ingredient per acre.

Materials and Methods

The sprays were applied to the densely weed-covered soil surface along and between the raspberry rows on 2 February, 15 March and 8 May 1959 at liquid volume rates of 40 gal./ac. by means of an Oxford Precision Sprayer. The plantation used was a discontinued experiment which had been planted in 1952 with the varieties Lloyd George and Malling Promise. Except for the barban treatments, which were tested on single plots, every treatment was applied to two plots each 9½ yards long and three rows in width. The treatments were as follows:

(a) *Applied* 10 *February:*

1. 1·0 gal. phenols.[1]
2. 3·0 gal. phenols.
3. 1·0 gal. phenols + 1·35 lb. fenuron.
4. 3·0 gal. phenols + 4·05 lb. fenuron.
5. 1·0 gal. phenols + 1·45 lb. fenuron + 2·5 lb. chlorpropham.
6. 3·0 gal. phenols + 4·35 lb. fenuron + 7·5 lb. chlorpropham.
7. 1·0 gal. concentrate of chlorinated phenols.
8. 3·0 gal. concentrate of chlorinated phenols.
9. 7·5 lb. dalapon + 4·8 lb. chlorpropham.
10. 4·8 lb. chlorpropham.
11. 6·0 gal. 60 per cent. stock emulsion tar oil + 2·0 lb. simazine.
12. 2·0 lb. simazine.
13. 7·5 lb. dalapon + 2·5 lb. amitrol in the form of non-activated 50 per cent. wettable powder.
14. 4·0 lb. monuron.
15. 1·5 lb. diquat and 3·0 lb. diquat (coded at the time by Plant Protection Ltd. as F.B.2).

(b) *Applied* 13 *March:*

16. 5·0 lb. amitrol in the form of non-activated 50 per cent. wettable powder.

(c) *Applied* 8 *May:*

17. 2·0, 4·0 and 6·0 lb. dalapon.
18. 2·0 and 3·0 lb. fenuron.
19. 4·0 and 8·0 monuron.
20. 1·0 and 2·0 lb. amitrol applied as an activated liquid formulation.
21. 2·5 and 5·0 lb. barban.[2]

The main constituent species of the weed carpet on all three spraying dates were *Stellaria media*, *Poa annua* and *Senecio vulgaris*, but other annual

[1] Materials 1-8 were formulated and supplied by the Mirvale Chemical Co. Ltd., Mirfield, Yorks, England. The 'phenols' were a mixture of higher boiling phenols.

[2] Supplied as Carbyne, 11·8 per cent. a.i. weight/volume, by Fisons Pest Control Ltd., Cambridge, England.

weeds germinated after the May spraying. Observations were made both on the weed flora and the crop on 16 February and at intervals thereafter until early August, covering periods of six months and three months for the earliest and latest treatments respectively.

Results

Of the treatments applied in February and March, only three combined good weed control with an absence of obvious crop damage. These treatments were:

2·0 lb. simazine,
4·0 lb. monuron,
3 gal. phenols + 4·05 lb. fenuron.

Each of these gave an excellent control of germinating seedlings, but the approximate time taken to kill the established weed growth varied from four weeks in the case of monuron to three months for simazine.

The phenol and chlorinated phenol treatments merely scorched the weeds, and had little or no effect as judged by the cover present two months after spraying. Wherever 4·8 lb. or more of chlorpropham was applied the growth of young canes was temporarily checked; and the dalapon/amitrol mixture, which destroyed the established weed flora, also caused some depression of new cane growth, especially in Lloyd George. The dalapon/chlorpropham mixture gave a good control of *Poa annua* and *Stellaria media* but not of *Senecio vulgaris*. Amitrol alone, applied in March, caused a chlorosis of the emerging young canes and gave only a temporary control of annual weeds. Diquat killed *Stellaria media* but had only a temporary scorching effect on well established *Poa annua*.

When simazine was applied in a mixture with tar oil the control of *Stellaria media* was as good as by simazine alone, but much of the *Poa annua* remained alive and green throughout the summer. No explanation is offered for this unexpected result. Both simazine alone and the simazine/tar oil mixture gave a complete kill of seedling weeds soon after germination.

The raspberries were severely damaged by all the May treatments. Dalapon caused some contact scorching followed by stunting of the new cane growth, with a chlorosis of the growing tips and a brownish discoloration and necrosis of the older leaves. Fenuron also caused contact scorching, with some stunting of the growth of new canes and fruiting laterals and a yellow marginal chlorosis of the lower leaves of the canes. With monuron, contact scorching was followed by interveinal leaf necrosis and apical deformity in the young canes which had received spray, and also by some necrosis of the fruiting laterals, but the growth of new canes recovered during the summer. Amitrol caused severe systemic damage, especially in Lloyd George, and barban a severe contact scorch without evidence of systemic action.

Discussion

Of the many materials tested in this short-term experiment, only simazine, monuron and a mixture of phenols and fenuron appear to deserve further trial. Used alone, the phenols constituent of the successful mixture scorched and killed some established weeds but showed no residual activity against germinating seedlings. It is therefore reasonable to assume, in the absence of evidence to the contrary, that the herbicidal potency of the mixture was due mainly to its fenuron constituent.

The use of monuron and simazine as residual herbicides for spring application to raspberry fruiting plantations and cane nurseries which are already weed-free has also been reported recently in preliminary papers from Mylnefield (Wood and Sutherland, 1960; Wood, Sutherland and Stephens, 1961; Sutherland and Stephens, 1961), where long-term experiments to test these treatments have given encouraging initial results. Similar work with simazine in Northern Ireland has been described by Robinson (1961), who earlier reported the use of monuron at 2 lb./ac. against established *Poa annua* in raspberries, a treatment which may have led to a slight reduction of yield in the following year (Robinson, 1960). It is possible that these or other materials, applied in late winter or early spring to plantations already clean, may remain active for long enough to suppress the weed growth that usually occurs in autumn, in which case low-rate maintenance applications to clean ground in spring may alone be required. Where a mat of overwintered annual weeds does develop, however, direct treatment with herbicides may be a valuable aid to normal cleaning methods, particularly where acreages are large or weather conditions unfavourable.

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SOME FACTORS REGULATING THE USE OF MALEIC HYDRAZIDE FOR RUNNER CONTROL IN STRAWBERRY PLANTATIONS

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SUMMARY

An experiment was done to investigate conditions under which maleic hydrazide fails to give adequate control of runners in strawberry plantations. In a second experiment the effect of applications of maleic hydrazide on flower initiation in the strawberry was studied.

One of the causes of reduced runner inhibition was thought to be the presence of runners already rooted at the start of treatment. To test this possibility, large plants of the variety Talisman were allowed to develop runner chains and were then treated with maleic hydrazide at 2, 4, 6 or 8 mg. per plant. Runners rooted when the experiment began were very resistant to inhibition and soon recommenced the production of secondary stolons. Stolons which had emerged but not formed roots at the time of treatment, however, were effectively inhibited, as were also those which emerged within two weeks of treatment. It is believed that when runner chains are present maleic hydrazide is translocated rapidly to the tips of the stolons, so that the duration and severity of runner control in other parts of the plant is greatly reduced in comparison to that obtained when the parent plants are free of rooted runners.

In the second experiment, in which the variety used was Auchincruive Climax, the formation of flower initials was inhibited by maleic hydrazide at concentrations which did not reduce the rate of leaf initiation. The effect did not persist for more than two plastochrons after treatment, and, provided that care is taken not to spray when flowers are being formed, this capacity for preventing flower truss initiation should not reduce the usefulness of maleic hydrazide for runner control.

INTRODUCTION

SINCE Denisen (1950) first reported that maleic hydrazide inhibited strawberry runner development, a number of papers have appeared describing the successful control of runners in strawberry plantations with this material (Denisen, 1953, 1956; Hitz and Brown, 1956; Hitz, 1959; Thompson, 1960, 1961).

Maleic hydrazide is usually described as a general growth inhibitor, but there can be no doubt that in the strawberry there are quite large quantitative

differences in the susceptibility of different parts of the plant to inhibition. It is because runners are particularly sensitive that their growth can be inhibited by maleic hydrazide without seriously inhibiting the growth of the parent crown. Successful control in the field depends on selecting a level of application of maleic hydrazide which gives this result as nearly as possible.

In practice it is found that the prevention of runner development over a period of from four to six weeks, which is the minimum for practical use, requires the application of a concentration which causes some visible damage to the parent plant for a week or two after treatment. However, Thompson (1960) found that even at levels which caused fairly severe chlorosis and a marked reduction of vigour in the parent plants, the size of the crop in the following year was not less than that from control plants from which all runners had been removed by hand. The main factor controlling the weight of fruit produced was the completeness of runner inhibition achieved, yield being highest in those treatments which had been kept free of runners, either by regular hand removal or by sprays of maleic hydrazide.

It was believed that the major cause of poor runner control in some treatments was the presence, before spraying, of a few rooted runners which were relatively resistant to inhibition and were able to produce chains of healthy secondary runners very soon after treatment. To test the effect of the presence of rooted runners on the development of later-formed runners, a model matted bed was set up and the parent plants were then treated with maleic hydrazide. The results of this experiment are described below.

Denisen (1953) reported a reduction in crop yield after spraying the strawberry variety Robinson with maleic hydrazide at 1,500 ppm. at the time of fruit bud differentiation. Klein and Leopold (1953) found some inhibition of flower initiation in Biloxi soybean, chrysanthemum and peppermint, but concluded that maleic hydrazide had inhibited flower initiation primarily through its effect on growth, rather than by any specific action against the photoperiodic mechanism. Because of the likelihood of crop loss if maleic hydrazide does suppress flower bud differentiation in the strawberry, plants of the variety Auchincruive Climax growing under flower inductive conditions in the glasshouse were treated regularly over a period of seven weeks with maleic hydrazide. The results of this experiment are also reported.

Effect of Runner Maturity and Position on Susceptibility to Maleic Hydrazide

Materials and Methods

In an earlier paper (Thompson, 1960) it was shown that the effectiveness of maleic hydrazide as a means of controlling runners decreased as the runner became more mature. It was concluded that for optimum inhibition in the field, maleic hydrazide should be applied when the first runners are visible but before they have started to root. In order to extend these observa-

tions a model matted bed was set up in pots in the glasshouse. Large plants of Talisman were used, each bearing 3 or 4 primary runners with runner chains of varying lengths. All rooted runners were pegged into pots of compost and allowed to establish themselves. The parent plants were then treated with maleic hydrazide (as the triethanolamine salt) at 2, 4, 6 or 8 mg. per plant, a control set of plants being left untreated. There were six plants in each treatment. Application was made by placing a 0·1 ml. drop of aqueous solution on a mature leaf of the parent plant and covering it with a cover slip until all traces of the solution had disappeared, about 30 hours later.

Results

The appearance of the parent plants and runners was carefully recorded, and one month after treatment the plants were harvested and the condition of the runners was recorded. The runners were divided into three classes:

(1) Those which were rooted at the start of the experiment.
(2) Those which were present at the start but had not formed roots.
(3) Those which did not emerge until after the date of treatment.

Runners in each class were recorded as 'inhibited' or 'uninhibited' according to their appearance at the time of harvest, 'inhibited' runners being those which had ceased to grow and did not appear likely to recover. Owing to the variations in the number and disposition of runners in different runner chains it was not possible to combine the records from different plants. Fig. 1 shows diagrammatically the condition of four successive runner chains arising from a typical plant treated with 6 mg. of maleic hydrazide, and illustrates the positions and classes of the runners inhibited by maleic hydrazide.

Runners of different classes varied in susceptibility to inhibition in a characteristic way, although the severity and duration of inhibition varied with the level of maleic hydrazide applied.

These results fully confirmed the ineffectiveness of maleic hydrazide on rooted runners. At no level—not even the levels at which the parent plants were severely inhibited—were more than a very few of the runners inhibited which had been rooted with at least one leaf fully expanded at the time of treatment. A few runners just forming roots, but without expanded leaves, were inhibited when the parent plant had been treated with either 6 or 8 mg. of maleic hydrazide, but many of these had begun to recover after periods varying from two to four weeks from treatment. Runners at this stage of development accounted for all the class 1 runners shown as inhibited in Fig. 1.

The stage of development reached by the runner was much more important than its position in the runner chain. This is shown clearly in Fig. 1. For example, practically all runners which had emerged but had not begun to form roots at the time of treatment were inhibited, as also were many of those which emerged very soon after treatment. As these were the youngest

runners, they tended to be furthest away from the point of application in the parent plant. There was no suggestion that rooted runners close to the parent plants were prevented from producing continuation stolons more than were rooted runners further away.

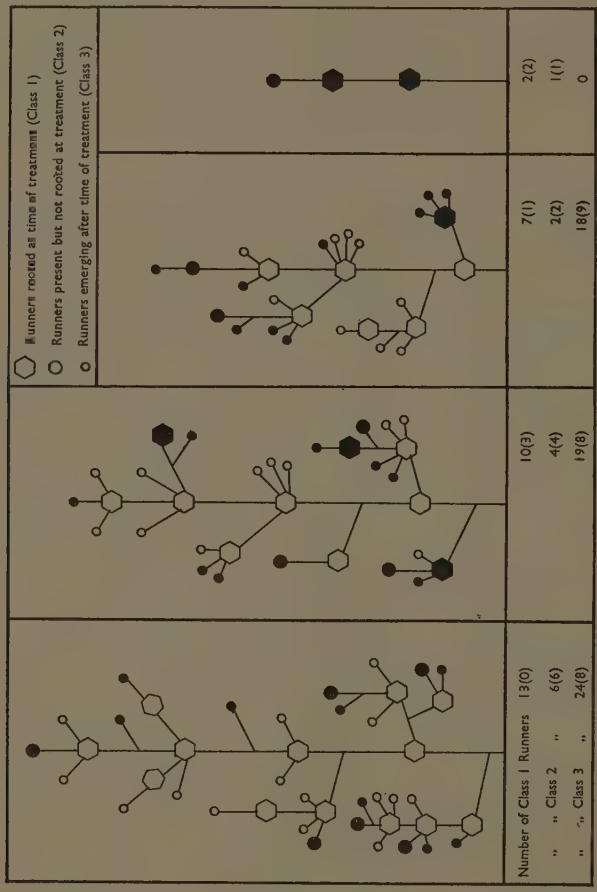

FIG. 1. Four successive runner chains produced by a plant of Talisman treated with 6 mg. of maleic hydrazide. Shading indicates inhibited runners at harvest-time, one month after treatment. Figures in brackets represent the number of runners of each class inhibited at this time.

The development of class 3 runners emerging from well rooted runner plants was checked for about two weeks after treatment, and at the three higher treatment levels runners emerging within this period were completely inhibited. After two or three weeks, however, new runners were again being freely produced by runner plants established before treatment, and, as may be seen from Fig. 1, quite large numbers of healthy uninhibited runners were present when the plants were harvested. Thus, an application of maleic hydrazide sufficient to give parent plants a very severe check was relatively

ineffective in checking new runner production from runners which had already rooted.

Effect of Maleic Hydrazide Treatment on Flower Initiation

Materials and Methods

Large plants of the variety Auchincruive Climax growing in pots, and each with two or three crowns, were moved into the glasshouse in July. This variety was chosen because it forms flowers regularly over a long period, and at the time of transfer to the glasshouse nearly all the crowns had already started to initiate flowers. Maleic hydrazide was applied as follows:—

(*a*) by dipping the youngest leaf into a solution containing:

(i) 250 ppm. or (ii) 125 ppm.

or (*b*) as an overall spray to the complete plant at:

(i) 125 ppm. or (ii) 62·5 ppm.

There were twenty plants in each treatment, and the experiment was divided into four blocks each containing five plants of each treatment and five untreated controls. The treatments were applied twice a week over a period of seven weeks, during which time each plant initiated an average of about five leaves. Rubber bands were placed over the leaves at intervals to provide a record of the rate of leaf emergence.

To record the effects of the treatments on flower initiation, batches of sample plants were dissected on three occasions: (i) immediately after the end of the treatments on 19 September, (ii) on 21 October and (iii) on 9 December. On each occasion one plant of each treatment was taken from each block. The first dissection was used simply as a check on the number of leaves initiated during treatment. The lengths of the petioles were measured and descriptions made of the appearance of the plants as records of the severity of inhibition resulting from treatment.

Results

The combined results of the second and third dissections are shown in Fig. 2, which is divided into sections to show flowers initiated before, during and after treatment. When treatment was started most of the crown buds contained flower trusses, and these can be seen between the third and sixth leaves emerging after treatment. During the period of regular treatment with maleic hydrazide all the crowns of the control plants initiated flowers, and practically the same was true for the plants treated with maleic hydrazide either as an overall spray at 62·5 ppm. or by dip to the youngest leaf at 125 ppm. With the spray treatment at 125 ppm. and the dip treatment at 250 ppm., however, flower initiation was almost completely prevented during this period, and with the second of these treatments practically no flowers were initiated until the third plastochron after the final application (leaf position 14). The results of the first dissections showed that the number of leaves in the bud did not vary with the treatments, nor did records of leaf

emergence show variations of more than one plastochron. There is, therefore, no possibility that the rate of leaf initiation was slowed down sufficiently to

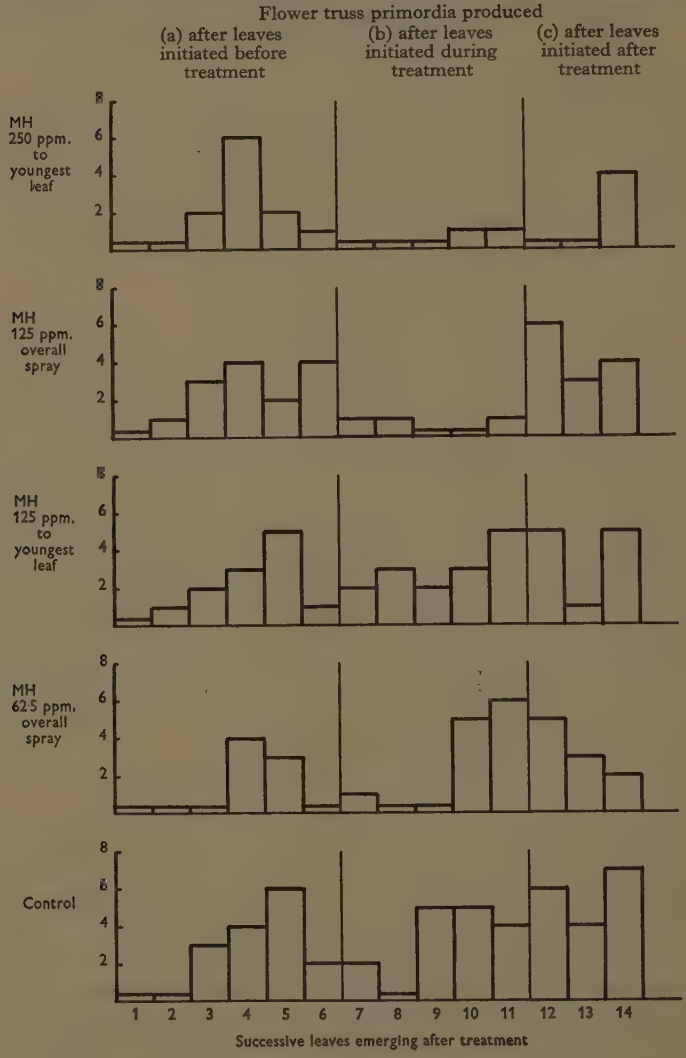
Flower truss primordia produced
(a) after leaves initiated before treatment
(b) after leaves initiated during treatment
(c) after leaves initiated after treatment
MH 250 ppm. to youngest leaf
MH 125 ppm. overall spray
MH 125 ppm. to youngest leaf
MH 62·5 ppm. overall spray
Control
8
6
4
2
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Successive leaves emerging after treatment

Fig. 2. Showing numbers of flower trusses found after each leaf position, in successive leaves emerging after the date of the first treatment with maleic hydrazide. (Vertical scale gives number of trusses found, as treatment totals, after each leaf.)

account for the absence of flowers during the period of treatment, and the results thus provide definite evidence that the higher levels of maleic hydrazide

inhibited the formation of flower initials without preventing the production and development of leaf primordia. It should be noted, however, that the higher levels of maleic hydrazide, which inhibited flower initiation, also quite severely reduced the length of the petioles of leaves which emerged during treatment, and caused a marked chlorosis of the laminae.

Discussion

The experiments described illustrate what are believed to be two of the major factors governing the use of maleic hydrazide for runner control in strawberry plantations. These are (i) its ineffectiveness against established runners, which are able to resume runner production very soon after treatment, and (ii) its inhibitory effect on the initiation of flower trusses, which may lead directly to loss of crop in the year following treatment.

It is likely that the first effect is due to two factors, one of these being the anatomical relationship between the runner and the parent plant. White (1927) showed that once runner plants have rooted they rely almost entirely for water and nutrients on their own roots, and that the paths of vascular connections along the stolons from the mother plant tend to by-pass the rooted runners and favour translocation along the chains formed by successive stolons. This means that material applied to the parent plant is most likely to be carried straight out to the tips of developing stolons rather than to be held in the rooted runner plants. This would account for the ability of rooted runners to produce healthy continuation stolons very soon after treatment. A second factor may be a dilution effect caused by the number of developing stolons present. Brown and Hitz (1957), in radioisotope tracer studies, showed that maleic hydrazide applied to the parent plant was very quickly translocated to the tips of the stolons, from which there was no tendency for it to be returned to the parent plant. In this way maleic hydrazide applied to parent plants bearing long chains containing numerous young unrooted runners is immediately dispersed to the ends of the stolons, and the inhibitory effect on the rest of the plant is greatly reduced. In practice it has been found most important to apply the first spray of maleic hydrazide before the first runners produced by the plants have started to root. If this stage is missed it is necessary to remove all rooted runners from the plantation before spraying.

These results suggest that the inhibitory characteristics of maleic hydrazide may make it more suitable for runner control in strawberries growing in rows as single plants than under systems where partial control only is required, as with plants growing in matted rows or matted beds. This possibility is supported by the fact that Denisen (1956), working with a matted bed, found it necessary to re-spray after ten days to achieve a high level of control in July and August, whereas Thompson (1960) did not need to re-spray for from four to six weeks when working with plants free of runners at the time of the first treatment.

Although the second experiment described above provides clear evidence that maleic hydrazide can prevent the formation of flower initials in the strawberry, the method of treatment adopted was not one which would ever be used in the field. However, a further experiment, in which plants of the varieties Talisman and Redgauntlet growing outside were twice sprayed at the time of flower-bud differentiation (in early September and early October) with maleic hydrazide at 500 and 1,000 ppm., also resulted in a significant reduction in flower truss initiation at the higher treatment level; but the inhibitory effects did not persist for more than one or two plastochrons.

Strawberry flower truss initiation in northern parts of Britain commences at the beginning of September, and to avoid reducing its extent it would be necessary to apply the last spray of maleic hydrazide for runner control not later than the middle of August. In practice it has been found that adequate runner control can be achieved when this precaution is observed, and, except in the case of perpetual fruiting varieties, there is reason to think that the chemical control of runners in strawberry plantations can be achieved without any reduction in the level of flower truss initiation in autumn.

The application of maleic hydrazide to plants bearing fruit is likely to lead to crop losses, and for this reason its use is confined either to maiden plantations deblossomed in their first year or to the period following the fruit harvest. Experiments testing maleic hydrazide to control runners in combination with simazine to control annual weeds have recently given promising results. It is hoped that the use of this or some similar combination of maleic hydrazide and a residual herbicide may obviate the necessity for summer cultivations in maiden strawberry plantations, which at present are a major factor in the labour requirements of the crop.

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Variety Trials of Vegetables in Scotland

VIII. SPRING-SOWN BRUSSELS SPROUTS, 1955-1961[1]

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Summary

Nine commercial varieties were compared for yield in spring-sown trials planted at Mylnefield in 1955-57, and ten were compared in 1958-60. In the second of these trial series the varieties were also compared for the size, firmness and colour of their sprouts and for proneness to external rotting and internal browning. There was a significant positive correlation in varietal incidence of these last two defects. Of the varieties tested, Irish Elegance is considered to be the most suitable for the fresh market and Sanda the best for quick-freezing. Both of these varieties and also Cambridge Special and Marché de Berne are suitable for private gardens. Two experimental F_1 lines raised at Mylnefield and included in the trial planted in 1960 gave firmer sprouts and significantly higher yields than any of the commercial strains.

Introduction

VARIETY trials of spring-sown brussels sprouts planted at Invergowrie during the period 1952-56 were described in an earlier paper (North and Frith, 1957). The results of four trials planted in 1957-60 are now reported here and the yields are compared with those in the 1955 and 1956 trials.

Methods

The trials were in randomized-block layouts with six replications, and in each replicate plot there were two rows of 32 plants. To see whether it might be possible to reduce the number of plants of each variety grown in future trials without undue loss of experimental precision, the yield of each row was recorded separately in the autumn of 1959. An analysis of variance of the results showed that the mean squares for error and within plots were very close to equality. This indicated that there was no appreciable component of variability between plots that could not be attributed to variation between halves of a single plot, and it seems that the precision of the mean yields for varieties was almost entirely dependent upon the number of

[1] Papers I-VII of this series appeared between 1956 and 1960 in the Annual Reports of the Scottish Horticultural Research Institute.

half-plots. Under the particular circumstances of the trial, therefore, the experimental precision depended largely on the total area allocated to a variety, and it mattered little how this area was sub-divided into replicate plots. This conclusion cannot be accepted as a generalization which holds true for all brussels sprout trials, but, since there was no evidence to suggest that it would be a clear advantage to alter the plot size in future trials, a layout similar to that of the previous trials was used in 1960.

Cultural treatments, and routine measures to control diseases and pests, were the same as those described in the earlier paper (North and Frith, 1957). Damage was caused by some diseases and pests which had not previously been encountered in the trials at Mylnefield. In 1957 approximately 6 per cent. of the total plants, including a higher proportion than this in the variety Atlas, wilted and died when they were about a foot tall: these losses were associated with the presence of *Phoma lingam* in the roots. In 1958 there was an unusually heavy attack of diamond-back moth (*Plutella maculipennis* Curtis), and in 1959 there were colonies of cabbage aphid (*Brevicoryne brassicae* Linné), which previously had rarely been seen at Mylnefield. Both of these pests were controlled satisfactorily by spraying with methyldemeton and D.D.T.

Special attention was given to the assessment of the quality of the sprouts in the trials from 1958 onwards. Firmness and size were measured by an instrument designed at Mylnefield (North and Frith, 1959), the measurements being made on 20 marketable sprouts selected at random from each plot. Sprout colour was assessed by eye on samples of 50 sprouts, by six independent observers. A scale of from 1 to 10 was used, in which 1 represented the lightest and 10 the darkest overall green colour.

In 1959 and 1960 50 marketable sprouts from each plot were cut open longitudinally to observe the incidence of internal browning. This defect, which cannot usually be detected from an external examination, is a necrosis of the leaves within the sprout, generally of those in the region centred on a line continued through the axis and lying midway between the growing point and the distal surface (Plate I).

Weights of marketable, rotten and frosted sprouts were recorded as in earlier trials.

Varieties Tested

In 1957 the same nine varieties were tested as in the trials previously reported for 1955 and 1956. In 1958, 1959 and 1960 the three varieties which had given the best performance in earlier trials—namely The Cluseed, Sanda and Cambridge Special—were re-tested with Cambridge No. 1 as a standard variety and with six varieties selected from the following on the basis of their performance in observation plots at Mylnefield:—

Champion, Des Granges, Evergreen, Freezer, Glasnevin Supreme, Holdbar Vinter, Irish Elegance, Irish Glacier, Jade Cross, Marché de

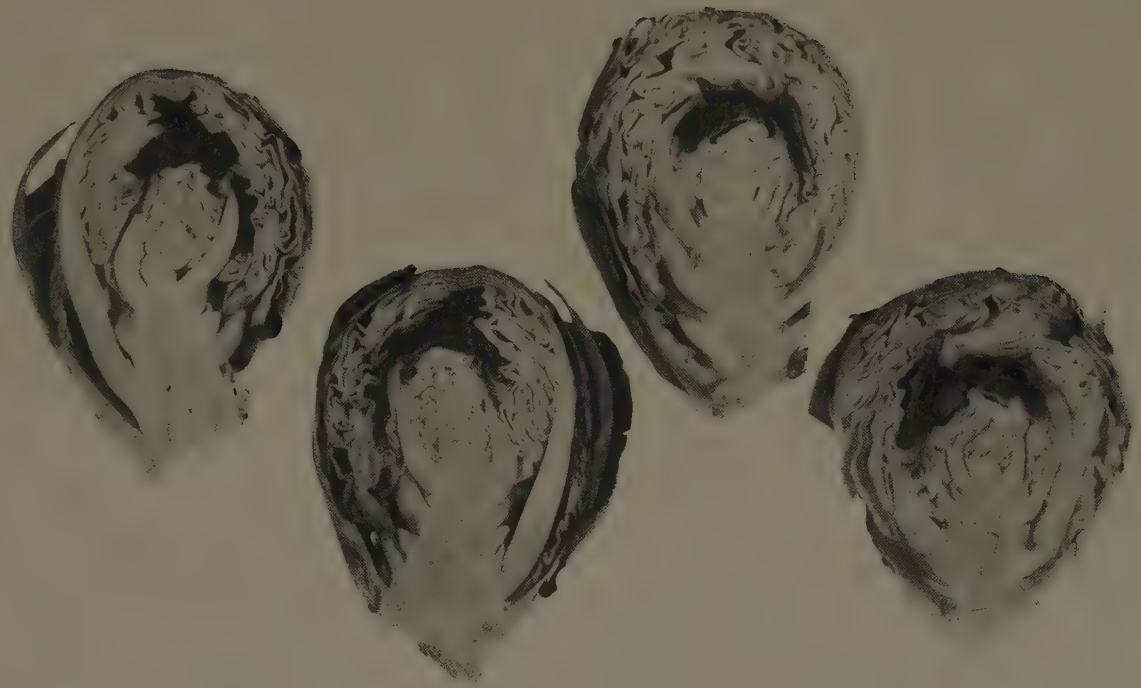


PLATE I. Brussels sprouts cut open longitudinally to show internal browning.

Berne, Masuda, Nain Special, Ny Kastrupgaard, Prominent, Polarstjerne, Rubine, Rapide, Sapidus, Solidity and Unicum.

In 1960 two experimental F_1 hybrid lines raised at Mylnefield were also grown in the trial. The purpose of including these was to determine what advantage in performance, if any, this type of seed stock might have over strains of brussels sprout produced by the conventional method of mass selection. These F_1 lines had been raised by saving the seed from ramets of a male-sterile clone grown in an insect-proof glasshouse together with plants of a uniform inbred male-fertile strain. The flowers were pollinated by honey bees, which were housed in small hives each containing three brood frames and heated from below by 25-watt electric light bulbs to make up for the deficiency of heat in the colony through housing so few frames in a single hive.

Results

Yields

Table I gives the recorded yields of marketable sprouts expressed as percentages of the yields of the control variety Cambridge No. 1 for the respective years. Yields for the trials planted in 1955 and 1956, which have already been reported, are included for comparison because these trials belong to the same series as the one planted in 1957.

Table I

Yields of marketable sprouts (combined October and March picks) expressed as percentages of the yields of Cambridge No. 1

Variety	*Year of Planting of Trial*					
	1955	1956	1957	1958	1959	1960
Mylnefield F_1 No. 1	—	—	—	—	—	370
Mylnefield F_1 No. 2	—	—	—	—	—	359
The Cluseed	118	133	124	147	125	187
Sanda	127	117	112	142	122	130
Cambridge Special	118	132	131	194	121	187
Atlas	106	124	91	—	—	—
Castricum Glory	122	105	95	—	—	—
Evesham Special	112	113	109	—	—	—
Grower B's	90	117	114	—	—	—
Cambridge No. 1	100	100	100	100	100	100
Grower A's	47	66	56	—	—	—
Marché de Berne	—	—	—	221	139	262
Irish Elegance	—	—	—	189	144	209
Irish Glacier	—	—	—	134	99	177
Glasnevin Supreme	—	—	—	129	106	164
Unicum	—	—	—	120	94	129
Solidity	—	—	—	93	74	55
LSD (P=0·05)	13	13	14	39	9	31
Yield of Camb. No. 1 (cwt./acre)	46	68	58	24	77	21

Each trial was harvested twice, in October and early March. The only figures given, however, are the combined yields for both picks, because varietal differences in yield in the March picks were inconsistent and usually not significant, whereas the ranking of varieties for yield in the October picks was similar to that for the combined picks.

In the 1955-57 trial series The Cluseed and Cambridge Special consistently gave yields significantly exceeding those of the control variety Cambridge No. 1, and the yields of Sanda were nearly as good. In the 1958-60 series the yields of these three varieties continued to exceed those of the control variety, but were equalled by those of Irish Elegance and exceeded by those of Marché de Berne. In 1960 both of the F_1 stocks gave yields significantly higher than those of any of the other varieties on trial, and three times as high as that of the control variety.

Sprout Characters

Table II gives data on the size, firmness and colour of the sprouts in the 1958-60 trial series. Mean figures for the size and firmness of the ten varieties are given for each of the trials, since these measurements are objective and may validly be compared between different trials. Corresponding mean figures for colour are not given, as assessments for this character are relative and subjective and can only be compared within any one trial.

TABLE II

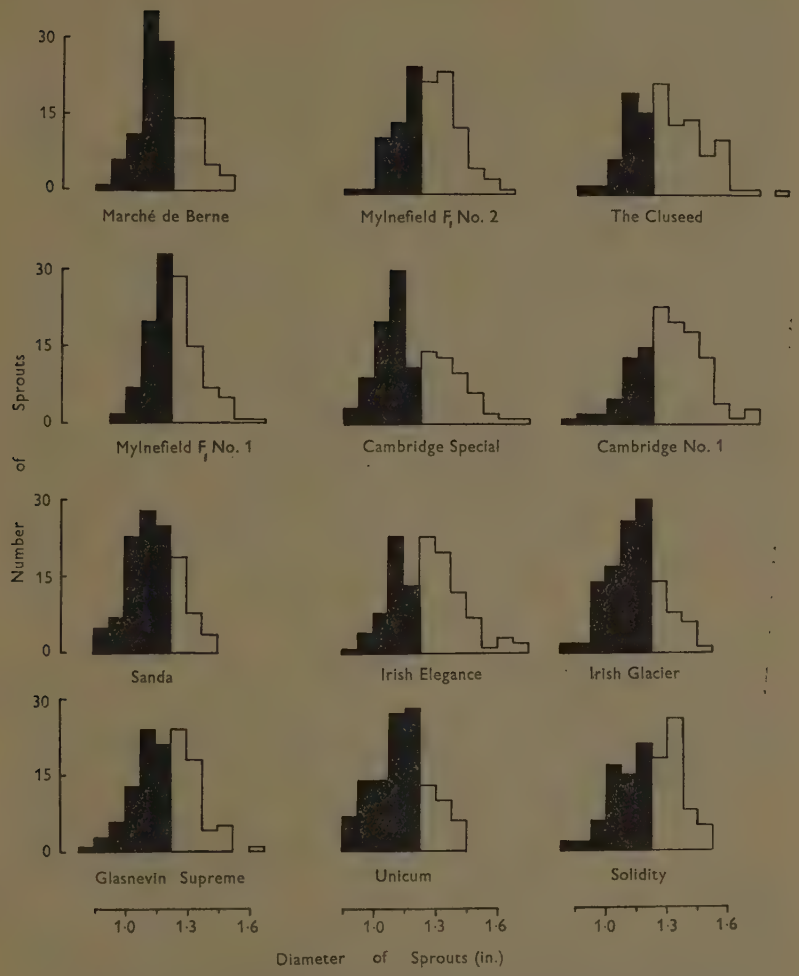
Sprout Characters

Variety (*Placing in order of average yield*)	*Size* (*Mean diam. in inches*)			*Firmness**			*Colour†*		
	1958	1959	1960	1958	1959	1960	1958	1959	1960
Marché de Berne	1·10	1·36	1·25	83	89	87	72	84	59
Irish Elegance	1·17	1·47	1·31	85	91	88	67	60	53
Cambridge Special	1·11	1·27	1·25	85	90	88	69	80	60
Sanda	1·01	1·30	1·20	84	90	87	78	81	73
The Cluseed	1·23	1·54	1·34	80	88	85	64	73	63
Glasnevin Supreme	1·06	1·37	1·26	82	91	88	73	78	58
Unicum	1·04	1·24	1·19	85	90	88	70	69	63
Irish Glacier	1·07	1·24	1·19	85	89	88	71	75	60
Cambridge No. 1	1·16	1·40	1·36	77	88	82	63	68	47
Solidity	1·13	1·39	1·26	74	83	81	65	61	61
LSD ($P=0·05$)	0·08	0·06	0·05	3	2	1	5	7	8
Mean	1·10	1·36	1·26	82	89	86			

Dates refer to the years in which the trials were planted.

* Diameter after compression expressed as percentage of diameter before compression.

† On scale 1-10 (1 lightest-10 darkest green) × 10.



TEXT-FIG. 1. Histograms showing the proportions of marketable sprouts of different size grades produced by varieties in the 1960 trial. The black columns show the numbers of sprouts which were of less than 1·22 in. diameter, and therefore small enough for quick-freezing. (Each histogram gives the size-grading of 120 sprouts.)

The commercial varieties which produced the firmest sprouts were Irish Elegance, Cambridge Special and Unicum, but in the 1960 trial one of the F_1 strains gave sprouts which were significantly firmer than those of any of the other varieties tested.

Sprout size varied appreciably according to the year in which the trial was conducted. This effect was so pronounced that in 1959 the mean size of the sprouts of all ten varieties was greater than that of the variety which produced the largest sprouts in 1958. Nevertheless, the ranking of varieties in respect of sprout size was fairly consistent from year to year. Relatively large sprouts were produced by The Cluseed, Irish Elegance, Cambridge No. 1 and Solidity, and small sprouts by Sanda, Irish Glacier and Unicum. Sprouts of other varieties were more or less intermediate in size.

Histograms showing the relative numbers of sprouts of different sizes in 1960 are given in Text-fig. 1. The areas shown in black indicate the numbers of sprouts which were less than 1·22 in. diameter, and therefore sufficiently small for quick-freezing. The varieties which gave the highest proportions of small sprouts in 1960 were Unicum, Sanda and Marché de Berne. These histograms also indicate the variation in the size of sprouts produced by any one variety. For example, those of The Cluseed and Cambridge Special were more variable in size than those of Marché de Berne and Sanda.

Table II also shows that varietal differences in sprout colour were fairly consistent. The sprouts of Sanda were about the darkest-green, those of Marché de Berne, Cambridge Special, Glasnevin Supreme and Irish Glacier

TABLE III

External Rotting and Internal Browning of Sprouts

Variety (*Placing in order of mean percentage of rotting*)	*External Rotting (in October pick only): Percentage by weight of total yield of sprouts from both picks*			*Internal Browning: Percentage of sprouts showing symptoms*	
	*1958	*1959	*1960	October 1959	March 1961
Irish Glacier	2·9	1·0	0·2	0·8	23·0
Unicum	4·8	1·9	0·1	0·8	3.0
Sanda	4·0	3·9	nil	3·3	6·0
Irish Elegance	4·2	3.7	0·7	2·5	10.0
Glasnevin Supreme	5·5	4.7	0·3	10·0	15·0
Solidity	3.0	12.4	nil	15·1	11·0
The Cluseed	4·6	12·6	0·7	3·3	5·0
Cambridge No. 1	5·5	13·0	0·7	20·0	23·0
Cambridge Special	8·1	20·6	1·0	13·3	24·0
Marché de Berne	7·5	24·1	2·7	13.3	10·0
Mean	5·0	9·8	0·6		
LSD (P=0·05)		2·8			

* Years in which the trials were planted.

fairly dark, and of those Cambridge No. 1, Solidity and Irish Elegance pale-coloured.

Table III gives data on the amount of external rotting of sprouts in the first picks of the 1958, 1959 and 1960 trials and on the amount of internal browning in the first pick of the 1959 trial and the second pick of the 1960 trial, occasions when this latter defect was prevalent. The figures for rotted sprouts are the weights of these, as recorded in the October harvests, expressed as percentages of the total yields of the respective varieties. Previously the amount of rotting had been measured by the total weight of rotted sprouts in both picks, expressed similarly as a percentage of total yield. Since, however, it was often difficult or impossible to distinguish in March which sprouts were rotted and which were frosted, the assessments for rotting made on this basis were often inconsistent. The new method of assessment shows fairly consistent varietal differences and is almost certainly more accurate than that used earlier.

Rotting was prevalent in 1959 and fairly pronounced in 1958, but only slight in 1960. Marché de Berne and Cambridge Special consistently gave higher proportions of rotted sprouts than other varieties, whereas the amount of rotting in Irish Glacier was somewhat less than the average. In both years the incidence of internal browning was relatively high in Cambridge Special and Cambridge No. 1, and low in Unicum, Sanda and The Cluseed.

Discussion and Conclusions

The yields given in Table I show that in both trial series some locally bred strains consistently produced only half the weights of marketable sprouts given by the most productive strains. It might be said in defence of these local strains that they were probably bred for growing as autumn-sown crops, as is customary in Scotland, whereas they were treated in these trials as spring-sown crops. It could be argued that had they been grown from autumn sowings their yields, in relation to those of other varieties, might have been higher. Unpublished results of experiments at Mylnefield to compare the behaviour of varieties sown at different seasons suggest, however, that this is unlikely, for in these experiments the yield ranking of five varieties remained fairly constant whether the seed was sown in spring or in autumn. It seems, therefore, that the yields in Table I give a reasonable measurement of the overall productivity of the varieties. The wide differences in yield indicate how extremely important it is to the grower that he should choose a good variety of brussels sprout; and they emphasize the fact that locally bred varieties should not be accepted as the best for the district unless they have proved their value in comparative trials.

The five most productive commercial varieties were Cambridge Special, Irish Elegance, Marché de Berne, Sanda and The Cluseed. Potential yield, however, is only one of the criteria to be taken into account when selecting a variety; sprout quality and size are both almost equal to it in importance.

The assessments of sprout characteristics given in Tables II and III deserve some comment. There is a fair measure of agreement in the varietal ranking for sprout size and firmness in each of the three trials, indicating clear varietal differences for these characteristics. Nevertheless, the average size and firmness for the ten varieties varied considerably from year to year. During the exceptionally warm year of 1959 the sprouts were larger and firmer than usual, and in the particularly cold season of 1958 they were smaller and softer. These results, however, should not be taken as an unqualified indication that sprouts are always larger and firmer in a warm season. Each year the sprouts were picked at approximately the same calendar date, so that in the warm season of 1959, for example, they were at a physiologically older stage of development than in a cold season. Thus the differences in average size and firmness are probably to some extent a reflection of the stage of development, and may merely be an expression of the fairly obvious fact that as the sprouts age they become larger and firmer.

Another interesting feature of the sprout characteristics shown in Table III is the apparent relationship between proneness to external rotting and to internal browning. Varietal differences in external rotting were fairly consistent during the three years of the trial, and the varietal ranking for external rotting corresponds closely to that for internal browning in 1959. To confirm this relationship, the correlation between percentage of rotted sprouts by weight and percentage of sprouts with internal browning was calculated for 1959 from the mean figures for the ten varieties grown in the trial and seventeen stocks of breeding material. A correlation coefficient +0·625 was found, which is significant at the 1 per cent. level. This result strongly supports the view that varieties which are susceptible to external rotting are also prone to internal browning. It does not imply that individual rotted sprouts usually have internal browning, or *vice versa*. In fact this is often not the case: the percentages of internally browned sprouts given in Table III were obtained from samples of apparently marketable sprouts

TABLE IV

Mean Values for Sprout Characteristics

Variety		**Size*	*Firmness*	*Colour*	*Rotting*	*Internal Browning*
Irish Elegance	(Large sprouts)	1·32	88·1	6·0	2.9	6·3
The Cluseed	(Large sprouts)	1·37	84·2	6·7	5·7	4·2
Cambridge Special	(Medium-sized sprouts)	1·21	87·8	7·0	9·7	18·6
Marché de Berne	(Medium-sized sprouts)	1·24	86·5	7·2	11·4	11·6
Sanda (Small sprouts)		1·17	86·9	7·7	2·6	4·6

* For explanation of headings, see Tables II and III.

taken at random after all unmarketable ones, including those which showed any signs of external rotting, had been discarded.

Mean values for the sprout characters of the five most productive varieties in the 1958-60 trial series are given in Table IV.

With the exception of the variety The Cluseed, which produces sprouts that are relatively soft and have few clear advantages for the fresh market over those of Irish Elegance, these varieties can be recommended for growing in the east of Scotland. The four recommended varieties may be described as follows:—

Irish Elegance

Bred by the late Professor Sherrard, of University College, Dublin, and available as Certified Original Seed grown from crops inspected by the National Institute of Agricultural Botany.

A very uniform strain, producing fairly tall plants with sprouts well spaced on the stem. The sprouts are medium to large in size and very firm, have a smooth surface, and are rather pale in colour.

This is a high-quality variety which is far superior to most others for the fresh market. Its only fault is the comparatively pale colour of the sprouts.

Cambridge Special

Bred by Mr. D. Boyes at the Cambridge University Horticultural Research Station, and available as Certified Original Seed.

The plants are usually rather variable in height but uniform in sprout characters. Most plants are of medium height and have sprouts which are closely packed on the stem so that they are sometimes difficult to pick. The sprouts are of medium size, have a smooth surface, and are very firm and of fairly good colour, but some are tinged with purple. They are prone to rotting and internal browning.

This is a productive, high-quality variety particularly suitable for gardens and allotments. It is sometimes grown for quick-freezing, but should be planted closely for this purpose because otherwise the sprouts become too large. Its main disadvantages as a variety for quick-freezing are its tendencies to purple coloration, external rotting and internal browning. Cambridge Special is unsuitable for autumn sowing, as it is prone to bolting.

Marché de Berne (Vatter Samen, Berne, Switzerland)

A fairly uniform strain, with plants of medium height. The sprouts are fairly well spaced on the stem and are of medium size, firm, and dark green in colour, and have a rather rough outer covering of leaves.

The main feature of this variety is its productivity. It is suitable for gardens and is of fair quality for quick-freezing provided that the plants are not too widely spaced. The sprouts are rather prone to rotting and internal browning. Marché de Berne is probably not suitable for autumn sowing, as it tends to bolt.

Sanda (C. Beemsterboer, Warmenhuizen, Holland)

A moderately uniform strain. The plants are fairly tall and produce small, fairly firm, very dark green sprouts which are well spaced on the stem. This variety is not prone to rotting or to internal browning, and may be autumn-sown.

The main value of Sanda is for quick-freezing, and for this purpose it was on the whole the best of the varieties tested. Its yield in 1960, however, was relatively low, and the appearance of the plants that year indicated that the stock tested was different from, and in some respects inferior to, that grown in earlier trials. This suggests that strains available in commerce under the name Sanda may vary in merit.

In the earlier paper on variety trials of brussels sprouts at Mylnefield (North and Frith, 1957) it was suggested that increases of yield in this vegetable could be obtained through increased vigour due to heterosis. The behaviour of the two F_1 hybrid lines clearly supports this contention, for both gave significantly higher yields than any of the other tested varieties. These two hybrid lines, however, were not raised from parents that had previously been carefully selected for maximum heterosis effect on their progeny. It is therefore reasonable to suppose that through a carefully planned selection of parent lines still greater improvements in yield might be obtained.

It was thought that it might be difficult to combine the advantages of large size and firmness in sprouts with increased vigour due to heterosis. However, the mean diameters of the sprouts of these F_1 hybrids were 1·31 and 1·29 in., figures which are about equal to that for the best large-sprouted variety, Irish Elegance: and the percentage figures for firmness of the sprouts of the two hybrids were 90·5 and 89·0, showing that they were firmer—one of them significantly firmer—than any of the other tested varieties.

The method by which the two F_1 hybrids were raised would not necessarily be economic on a commercial scale. However, less costly techniques for the production of heterosis seed of brussels sprouts for Scottish conditions are being examined at Mylnefield.

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RASPBERRY VIRUSES AND VIRUS DISEASES IN BRITAIN

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SUMMARY

In Britain the raspberry suffers from some viruses that are soil-borne, others that are insect-borne, and still others whose mode of spread is unknown.

The soil-borne viruses—arabis mosaic, raspberry ringspot and tomato black ring—have ectoparasitic nematodes as vectors and are widely though locally distributed. Some varieties of raspberry are susceptible to one or more of them and develop severe stunting diseases, whereas others are immune from infection. Current knowledge of these viruses is briefly surveyed.

The aphid-borne viruses are mostly transmitted by *Amphorophora rubi* Kalt., and these divide into two groups, (*a*) heat labile and (*b*) heat stable, according to their ability to multiply in infected raspberry plants kept at 37° C. Viruses of group (*a*) cause necrosis in *Rubus occidentalis* and *R. henryi* and are sap-transmissible from *R. occidentalis* to non-Rubus hosts: they cause characteristic leaf symptoms in some raspberry varieties but vague or no leaf symptoms in others. The group probably comprises a number of similar viruses or virus strains. Group (*b*) includes Rubus yellow net virus, which, in conjunction with viruses of group (*a*), causes raspberry mosaic disease, and a number of ill-characterized viruses which cause leaf-yellowing diseases of raspberry. The viruses of both groups are of the non-persistent type; aphids acquire them in 1-2 hr. feeding on infected plants but retain infectivity for only 4-5 hr. Little is known of the vector relationships of vein chlorosis, a heat-stable virus transmissible by *Aphis idaei* v.d.G. but not by *A. rubi*. Raspberry varieties differ greatly in susceptibility to infection by these various viruses and some resist colonization by *A. rubi*.

Rubus stunt, a dwarfing disease of raspberry and other *Rubus* spp., occurs in southern England and in the Netherlands, where a leafhopper vector, *Macropsis fuscula* Zett., has been found. The virus seems to have a long latent period and to persist in its vector.

Diseases of which the etiology and mode of spread are still unknown include bushy dwarf, curly dwarf and yellow blotch. The first of these is associated with a sap-transmissible virus, the properties of which are described and which resemble those of tomato spotted wilt virus.

Introduction

IN many ways the raspberry is a remarkable plant. It must be among the oldest and most widely grown of domesticated fruits and is one that remains astonishingly productive under the vilest of cultural treatments and despite infection by innumerable different viruses. Through the years, the plant breeder's art has transformed the humble wild raspberry into a fruit of noble proportions, if often of pallid flavour. Levels of productivity have risen even further as a result of the efforts, during the past forty years, of a handful of workers in Europe and North America to study the viruses that infect the raspberry, and to devise means of preventing the losses they cause. These viruses include some that spread through the soil, others transmitted by aphids or by leafhoppers, and still others transmitted by agents as yet undiscovered. Most of them occur wherever raspberries grow, whether cultivated or wild, but exact knowledge of all but a few is scant. This is especially true of the aphid-borne viruses, easily the commonest and most widespread causes of disease. Progress depends upon the evolution of better techniques of studying them. This demands time and a degree of application which few can afford, so that it is small wonder that raspberry viruses have remained an esoteric field of research.

Many virus diseases of raspberry live on in the literature although the material from which they were described has long since died. The etiology of others is confused through the identification of virus diseases with viruses, lack of appreciation of the pitfalls of symptomatology, and the use of names that suggest relationship where mere analogy exists. The invitation to write this review offered an opportunity to take stock of the information on raspberry viruses and virus diseases described from Britain and to provide a reference point for further work on an ill-understood group of viruses. For convenience, the viruses are grouped according to their mode of spread.

Soil-borne Viruses

Outbreaks of a lethal disease, which seemed to occur spontaneously in plantations of Baumforth's Seedling raspberry, were first noticed in eastern Scotland in 1922. With the rise in popularity of the Lloyd George variety the disease disappeared, but in 1941 Mr. N. H. Grubb, then at East Malling Research Station, found a similar disease in plantations of the variety Norfolk Giant in Angus and east Perthshire. The spectacular nature of the outbreaks caused alarm and prompted investigations which showed that the disease was graft-transmissible and of virus origin. It was named leaf curl by Harris, Bryce and Foister (1943) because of its resemblance to the aphid-borne North American disease of the same name. Persistent search during the next ten years failed to reveal an insect vector, and although clues as to its mode of spread existed, these were ignored or misinterpreted. The disease remained an enigma until 1953, when a sap-transmissible virus, named raspberry ringspot, was demonstrated as the cause (Cadman, 1956)

and found to be transmitted through the soil (Harrison, 1956). These experiments revealed the existence of another soil-borne virus of a similar type, named beet ringspot virus by Harrison (1957), which was first found infecting raspberry (Malling Seedling V) in Angus in 1956 (Harrison, 1958*c*).

In 1954 Mr. F. A. Roach sent samples of Malling Exploit raspberry, affected by a severe disease, from Bere Ferrers, south Devon, and from these a third virus was isolated (Cadman, 1956) which also proved to be soil-borne and was later named raspberry yellow dwarf virus (Harrison, 1958*b*) because of the distinctive symptoms it caused in Malling Exploit raspberry. Ecto-parasitic nematode vectors have subsequently been discovered (Table I) for raspberry yellow dwarf virus [*Xiphinema diversicaudatum* (Micol.): Jha and Posnette 1959; Harrison and Cadman, 1959] and beet ringspot virus [*Longidorus elongatus* (de Man): Harrison, Mowat and Taylor, 1961], and discovery of a nematode vector for raspberry ringspot virus seems only a matter of time.

TABLE I

Properties of nematode-borne viruses infecting raspberry

Virus	*Particle shape and size*	*Thermal end-point* °C	*Nematode vector*	*Disease caused*
Arabis mosaic	Isometric	58–61	*Xiphinema diversicaudatum* Micol.	Raspberry yellow dwarf
Raspberry ringspot	Av. diam. 29–30 mμ	66–70	—	Raspberry leaf curl
Tomato black ring, beet ringspot strain		60–63	*Longidorus elongatus* de Man	Unnamed

It is now well known that these three viruses, although serologically unrelated, share many biological and physical properties, infect a wide range of crop and weed plants, and occur in soils in many parts of Britain and continental Europe (Harrison, 1960). For these last two reasons, it is hardly surprising that each of the viruses has been described before from other hosts. Thus, serological tests have shown that raspberry yellow dwarf virus is closely related to the arabis mosaic virus described by Smith and Markham (1944) (Cadman, 1960*b*), and that beet ringspot virus is a strain of tomato black ring virus (Smith, 1946; Harrison, 1958*a*). Although serological evidence is lacking, it is virtually certain that raspberry ringspot virus (Cadman, 1956) is a strain of the red currant ringspot virus described by Klesser (1951).

Outbreaks of disease caused by these viruses in raspberry seem closely correlated with the presence in soils of their nematode vectors, but little is yet known of the behaviour of the viruses in their vectors. *X. diversicaudatum* has not yet been found in Scotland and, in raspberry, arabis mosaic virus has occurred only in plants imported from England, where both nematode and virus are widespread. On the other hand, although raspberry ringspot and tomato black ring viruses occur in soils in several parts of England, they are important causes of disease in raspberry only in eastern Scotland. This is possibly because raspberries are grown more extensively in eastern Scotland than anywhere else in Britain. However, Scottish strains of the viruses are only distantly related serologically to English ones (Harrison, 1958*a*; Cadman, 1960*b*), and there is evidence, with tomato black ring virus, that different strains have different vectors. *L. elongatus* is a vector of Scottish strains of the virus, but the lettuce ringspot strain, found in Norfolk, is transmitted by *L. macrosoma* Hooper (Harrison, Mowat and Taylor, 1961). Possibly the nematodes have different host preferences and these account for the apparent absence of the virus in raspberry in England. Although raspberry ringspot virus occurs in cherry in several districts of Kent, the virus has never been found in raspberry there; yet plants of Malling Jewel raspberry became infected when grown at a site in Wiltshire where the

TABLE II

Reactions of raspberry varieties to infection by arabis mosaic (AMV), raspberry ringspot (RRV) and tomato black ring (TBRV) viruses

Raspberry variety	*Virus*		
	AMV	RRV	TBRV
Baumforth's Seedling A	...	−	...
Baumforth's Seedling B	...	+	...
Burnetholm Seedling	−	−	+
Lloyd George	−	−	−
Malling Enterprise	−	+	−
Malling Exploit	+	+	+
Malling Jewel	−	+	−
Malling Landmark	(−)	−	−
Malling Notable	−	+	−
Malling Promise	−	+	−
Malling Seedling K	(−)	+	+
Malling Seedling M	(−)	−	−
Malling Seedling V	(−)	−	+
Norfolk Giant	−	+	+
Preussen	...	+	...
St. Walfried	...	+	...

− = immune.
(−) = probably immune but reaction unverified.
\+ = susceptible.
... = not tested.

virus occurred in the soil (Harrison, 1958*c*). These anomalies will no doubt be resolved by further studies. None of the viruses has been found infecting raspberry in continental Europe, although both the viruses and their vectors occur there.

Raspberry varieties differ greatly in their reactions to the three nematode-borne viruses: one is susceptible to all three, whereas others are immune from one or more (Table II). Varieties found immune (by graft test) to Scottish strains of raspberry ringspot and tomato black ring viruses have never been found infected with these viruses in the field in eastern Scotland, but no tests have been made with other strains of the viruses. Little is known of the nature of this immunity, except that it is heritable and that immunity from each of the viruses is probably a dominant character inherited in a simple manner (Jennings, 1960).

Susceptible varieties differ in proneness to infection and, once infected, in the symptoms they show. 'Raspberry yellow dwarf' is descriptive of the disease caused by arabis mosaic virus in Malling Exploit, so far the only variety found susceptible to it. 'Leaf curl' is a less happy choice of name for the disease caused by raspberry ringspot virus, for only the varieties Baumforth's Seedling B and Norfolk Giant show the typical symptoms described by Harris, Bryce and Foister (1943). Conspicuous chlorotic ringspot patterns on the leaves are characteristic symptoms of infection in these and other susceptible varieties, and usually develop the year after plants first become infected. Chronically infected plants of Baumforth's Seedling B, Malling Enterprise, Malling Jewel, Malling Notable, Norfolk Giant and Preussen produce stunted, brittle canes and usually die within two years of infection. The other susceptible varieties listed in Table II tolerate infection; chronically infected plants are usually less vigorous than healthy plants of the same variety but may show few or no characteristic leaf symptoms. The disease caused by tomato black ring virus in raspberry has never been named. The symptoms in susceptible varieties are indistinguishable from those produced by raspberry ringspot virus, and it might, indeed, be less confusing if the name 'leaf curl' were abandoned and raspberry ringspot disease used to denote diseases caused either by raspberry ringspot or by tomato black ring viruses.

Nematode-borne viruses are of local importance in raspberry, and outbreaks of the diseases they cause vary from square yards to a few acres in extent. The devastation in plantations of susceptible varieties is often spectacular, but the consequences of propagating tolerant varieties on land containing the viruses are more far-reaching. Because they infect so many different kinds of plant and are seed-borne in many common weed species (Lister, 1960), nematode-borne viruses present special problems of control. More knowledge of the ecology of both the viruses and the nematodes is needed, but successful control may well be easier to achieve by eliminating sources of infection rather than by the use of chemicals to kill the nematodes. With raspberry, fortunately, these problems are avoidable by the planting

of immune varieties, and there seem good prospects of breeding new sorts that will combine virus immunity with commercial usefulness.

Raspberry roots commonly contain tobacco necrosis viruses and occasionally become infected with tobacco rattle virus. None of these viruses seems to invade or produce symptoms in the tops of plants.

Aphid-borne Viruses

Although aphids were shown to transmit viruses infecting raspberry in North America as long ago as 1922, evidence that they are vectors of similar viruses in Europe was not obtained until 1947 (Cadman and Hill, 1947). In both continents, the aphids concerned are species that normally spend their entire life cycle on raspberry. In Europe, these are *Aphis idaei* v.d.G. and *Amphorophora rubi* Kalt. Each is ubiquitous on wild and cultivated raspberry and each transmits viruses which the other does not.

Viruses transmissible by Aphis idaei

Cadman and Hill (1947) found that plants of Norfolk Giant raspberry developed chlorosis of the finer leaf veins when colonized by *A. idaei* that had previously fed on diseased Lloyd George plants. The symptoms in Norfolk Giant were named vein chlorosis and shown to be caused by a virus transmissible by *A. idaei* and not by *A. rubi* (Cadman, 1952*a*). Aphids acquired the virus in 12 hr. feeding on infected Lloyd George plants, but the time for which they remained infective was not determined. Working with *A. idaei* and an apparently identical virus occurring in Lloyd George in Canada, Stace-Smith (1961) has found that aphids lose infectivity within 24 hr. when feeding on raspberry. *A. idaei* is troublesome to handle, and an obstacle to further work is the lack of a test plant susceptible to the virus and acceptable to the aphid.

Raspberry plants can be freed from infection by some kinds of aphid-borne viruses, but not from infection by vein chlorosis virus, by being kept for a few weeks at 37° C (Stace-Smith, 1960; Chambers, 1961). This virus has not been transmitted mechanically from raspberry to herbaceous plants and there is no other information on its properties. It is widespread in both cultivated and wild raspberry in Europe, and strains, differing in virulence, have been differentiated on symptoms and the results of plant-protection tests (Cadman, 1952*a*). Most European raspberry varieties display characteristic symptoms when infected but differ in susceptibility to infection. There are indications that some North American varieties may be immune from infection: plants of Cuthbert, Newburgh and Viking raspberry failed to become infected when grafted with infected Norfolk Giant scions (Cadman, 1952*a*).

Viruses transmissible by Amphorophora rubi

Without doubt, *A. rubi* transmits many viruses that infect raspberry, but

study of them is beset by many difficulties. Most cultivated raspberry varieties resist infection by these viruses to a degree which makes them useless for experimental work. By contrast, the North American black raspberry, *Rubus occidentalis L.*, is at first sight an almost ideal test plant. When seeds can be induced to germinate (sometimes no mean feat), large numbers of uniform seedlings can be raised, and these develop symptoms within days, or at most a few weeks, of being colonized by infective aphids. High rates of transmission are obtainable with 1-5 infective aphids per plant.

There the advantages mostly end. It seems that all the viruses transmitted by *A. rubi* have similar relationships with their vector. Aphids acquire the viruses in ½-1 hr. feeding on infected plants but remain infective for only a few hours. Mixtures of viruses cannot readily be separated unless the aphids are transferred at frequent intervals to fresh healthy seedlings. The results from this kind of experiment vary with the strain of *A. rubi* used. To many strains of the aphid, *R. occidentalis* is an unpalatable plant, and their efficiency as vectors diminishes rapidly the more often they are disturbed. For the same reason, transmission of viruses from diseased to healthy *R. occidentalis* is difficult or impossible to obtain, and this also militates against the separation of virus mixtures. Finally, despite their high susceptibility to infection, *R. occidentalis* plants develop identical symptoms when infected with apparently different viruses. So far only one virus, Rubus yellow net (Stace-Smith, 1955*a*), is known to produce distinctive symptoms.

Most progress in the analysis of this group of viruses has been made in Canada by Stace-Smith, where the North American form of *A. rubi*, perhaps because it thrives on *R. occidentalis*, acts as an efficient vector. There is much evidence to suggest that the viruses isolated in British Columbia are the same as, or closely related to, some that occur in Europe, but also much to indicate that fewer viruses occur there than in Europe, or indeed than in other parts of North America.

The results of exposing virus-infected raspberry plants at 37° C show that the viruses transmissible by *A. rubi* fall into two groups. Some are unable to multiply in plants at this temperature, whereas others survive even when infected plants are kept for 6 weeks or more at 37° C (Stace-Smith, 1960; Chambers, 1961). There is evidence also that the heat-labile viruses are mechanically transmissible from infected *R. occidentalis* and *R. idaeus* to herbaceous test plants, whereas the heat-stable viruses are not (Cadman, 1960*a*).

HEAT-LABILE VIRUSES

All the viruses in this group produce necrosis and leaf mottling in *R. occidentalis* and necrosis of shoots of *R. henryi*, and there is little evidence to show whether they are merely different strains of one virus or a group of unrelated viruses. The viruses produce characteristic leaf symptoms in some raspberry varieties but indistinct or no symptoms in others, and some

have been given distinctive names: for example, raspberry leaf mottle (Cadman, 1951), raspberry leaf spot (Cadman, 1952*d*) and black raspberry necrosis (Stace-Smith, 1955*b*). Evidence that these names denote viruses and not merely virus diseases is slender.

Table III shows the results of an experiment in which Norfolk Giant plants infected with leaf mottle virus, and Malling Landmark and St. Walfried plants infected with latent viruses, were grafted with scions of sister plants of the same varieties or with scions from plants of other varieties all infected with heat-labile viruses that produced necrosis in *R. occidentalis* and *R. henryi*. Plants of the indicator varieties displayed different symptoms when grafted with scions of each of the infector varieties listed. This may imply absence of protection, and hence of relationship, between the viruses, but it is doubtful if the results bear this interpretation. When *A. rubi* are fed on Norfolk Giant plants infected with leaf mottle virus, for example, and transferred to *R. occidentalis* seedlings, these develop symptoms ranging from necrosis to mild leaf mottling. The same applies with the other infector sources listed in Table III, and there is no evidence to show whether this variation reflects differences in the *R. occidentalis* test plants or indicates the existence of a mixture of viruses in the infector plants.

TABLE III

Reactions of raspberry varieties to infection with heat-labile viruses

Infector variety	*Virus present in infector*	*Indicator variety*		
		Norfolk Giant	Malling Landmark	St. Walfried
Norfolk Giant	Leaf mottle	−	+	+
Malling Jewel	Leaf spot	+	−	−
Lloyd George	Latent	−	+	+
Malling Landmark	Latent	−	−	+
Malling Promise	Latent	−	+	+
St. Walfried	Latent	−	+	−

− = no leaf symptoms. + = characteristic leaf symptoms.

A recent discovery (Cadman, 1960*a*) offers a hopeful new approach to this problem. Viruses have been transmitted mechanically from *R. occidentalis* plants infected, by means of *A. rubi*, with viruses from the following raspberry varieties: Lloyd George, Malling Exploit, Malling Jewel, Malling Landmark, Malling Promise and Norfolk Giant. The viruses produce local lesions and systemic symptoms in *Chenopodium amaranticolor* Coste & Reyn. and *C. quinoa* Willd., and infect but produce no symptoms in *Datura stramonium* L. and *Petunia hybrida* Vilm. The viruses seem to reach only low concentrations in both *R. occidentalis* and herbaceous plants. Little

is yet known of their properties, and none of them have so far been transmitted from infected herbaceous plants to *R. occidentalis* or *R. idaeus*.

The importance of these heat-labile viruses is difficult to assess at present. It seems very likely that they are responsible for many of the ill-defined and evanescent leaf symptoms found in commercial plantings of many varieties of raspberry, and that their presence in plants accentuates the symptoms produced by other viruses (see below). They are widespread in both cultivated and wild raspberry, and mixtures of them produce the disease in Baumforth's Seedling B and Norfolk Giant called Mosaic 2 by Harris (1940). Plants freed from the viruses by heat treatment usually produce large, symptomless leaves and grow more vigorously than infected plants, and there is evidence from Malling Jewel and Lloyd George that virus-free plants yield more fruit than infected ones (Wood, 1960).

Cadman and Fisken (1958) found that raspberry varieties differed in the rate at which they became infected with leaf spot virus when exposed to infection spreading from diseased Lloyd George plants. After 2 years' exposure, the proportions of plants (50 per variety) of different varieties which became infected were: Lloyd George 90 per cent., Malling Exploit 87 per cent., Malling Promise 72 per cent., Malling Landmark 22 per cent. and Norfolk Giant 0 per cent. The last two varieties are interesting because their behaviour exemplifies two kinds of resistance to infection by aphid-borne viruses, each genetically controlled, which are now being used by plant breeders in Britain. Malling Landmark resists colonization by *A. rubi* whereas Norfolk Giant does not, although it evidently resists infection by leaf spot virus. There seem good prospects of breeding raspberry varieties that possess resistance to *A. rubi* as well as to infection by the viruses it transmits (Knight and Keep, 1958; Jennings, 1960).

Although uncommon in raspberry, cucumber mosaic virus is logically included here because it is transmissible by *A. rubi* and is heat-labile (Harrison, 1958*d*; Kassanis, 1954). It has been found infecting Lloyd George raspberry in several plantations in eastern Scotland but appears to spread little. Infected plants showed large light and dark green blotches on their leaves, and cucumber mosaic was transmitted from them by mechanical inoculation of sap but not by means of *A. rubi* or *Myzus persicae* Sulz. Both kinds of aphid transmitted the virus from infected *Datura stramonium* to *R. occidentalis* (Harrison, 1958*d*).

HEAT-STABLE VIRUSES

Apart from vein chlorosis, plants of most European raspberry varieties commonly show two other kinds of leaf symptom; these have been called veinbanding (Cadman, 1952*b*) and yellows (Cadman, 1952*c*). The viruses which produce these symptoms persist in infected plants kept for 6-8 weeks at 37° C, and are thus differentiated from the heat-labile viruses (Stace-Smith, 1960; Chambers, 1961).

Veinbanding disease: Perhaps because of its commonness, everyone who has worked with raspberry viruses seems to have felt obliged to coin a new name for this disease. The names range from raspberry mosaic (Rankin, 1927), by far the most descriptive, to green mottle mosaic (Cooley, 1936), Rubus virus 1 (Smith, 1937), *Marmor rubi* (Holmes, 1939), mosaic 1 (Harris, 1940) and veinbanding (Cadman, 1952*c*). Cadman believed that the symptoms he called veinbanding were caused by one virus, but Stace-Smith (1956) showed that the analogous raspberry mosaic disease in British Columbia was caused by two viruses: one heat-labile (black raspberry necrosis virus) and the other heat-stable (Rubus yellow net virus). Both viruses were transmissible by, and had similar relationships with, *A. rubi*, but could be separated from one another either by keeping infected raspberry plants at 37° C or by allowing infective *A. rubi* to feed for short periods on a series of *R. occidentalis* seedlings. Whilst visiting Britain in 1958, Stace-Smith (unpublished) showed that veinbanding-infected Norfolk Giant and Malling Jewel plants contained at least two components, one of them apparently identical with Rubus yellow net virus. A similar virus was isolated from a diseased Norfolk Giant plant that had been freed from leaf mottle virus by heat treatment. Although confirmation is needed, it is virtually certain that the heat-stable viruses isolated in British Columbia and Scotland are the same, or at least closely related. The veinbanding virus of Cadman (1952*b*) is therefore a misconception, and it would be as well to abandon the name 'veinbanding disease' in favour of raspberry mosaic (Stace-Smith, 1956).

Like leaf mottle and black raspberry necrosis viruses (Cadman, 1954; Stace-Smith, 1955*b*), Rubus yellow net virus is acquired by *A. rubi* in ½-1 hr. feeding on infected plants and persists for only a few hours in its vector. Symptoms (chlorosis of the finer leaf veins) take 3 or more weeks to develop in infected *R. occidentalis* plants, as against 5-7 days for the other two viruses (leaf mottle and black raspberry necrosis). In leaves of Norfolk Giant it produces a mild, net-like chlorosis; its effects on virus-free plants of other raspberry varieties are unknown.

Raspberry mosaic is among the commonest diseases of raspberry in Britain, and symptoms in most varieties are conspicuous. These vary greatly in severity, doubtless because of variation in the number and kind of other viruses present in plants along with the yellow net virus, but symptom expression is also much affected by environmental conditions. Raspberry varieties differ in susceptibility to infection. Malling Jewel and Lloyd George are more susceptible than Norfolk Giant, Malling Promise and Malling Exploit, but even in Lloyd George the disease spreads only slowly in eastern Scotland despite the abundance there of *A. rubi* (Cadman and Fisken, 1958).

Yellows diseases: Bronzing and yellowing of leaves on the fruiting canes and/or the lower leaves of young canes are common symptoms in many varieties of raspberry. Indeed, one or two kinds, no longer in cultivation, were recognizable on sight because all plants produced yellowed leaves.

Some of these diseases are caused by viruses, and Cadman (1952*c*) described two in Norfolk Giant which he named mild and severe yellows because they appeared to protect against infection by one another in graft tests. Chambers (1961) found that symptoms of mild yellows persisted in infected Norfolk Giant plants kept for 6 weeks at 37° C. These viruses are thought to have aphids as vectors but this still needs confirmation.

Many other kinds of leaf yellowing are known in raspberry but their etiology has never been established, largely because of lack of a suitable differential host plant and the absence, until recently, of virus-free raspberry plants. It seems unlikely that diseases of this kind are unique to Europe, but none similar have been described from North America.

Leafhopper-borne Viruses

Raspberry is one of the hosts of a virus which Prentice (1950) found in southern England and named Rubus stunt virus, because of the symptoms it produced in wild and cultivated Rubi. Infected plants typically produce tufts of weak, spindly canes, and fruiting laterals that are slow to develop and often have abnormal, leafy and sterile flowers. Raspberry varieties differ much in their reactions to infection, and a few, such as Norfolk Giant, take more than a year to develop symptoms. An apparently similar virus which occurs in the Netherlands is transmitted by the leafhopper *Macropsis fuscula* Zett. (de Fluiter and van der Meer, 1953). The leafhopper has only one generation a year, and most spread of virus seems to occur in July and August. There is evidence that the virus has a long latent period (30 days or more) in its vector (de Fluiter and van der Meer, 1956). In southern England the virus seems commoner in wild and cultivated brambles than in raspberry, and two species of *Macropsis*, *M. fuscula* and *M. scotti* (Edw.), have been found to act as vectors (Legg, unpublished). The virus does not occur naturally in raspberry or *Rubus* spp. in Scotland.

Virus Diseases Transmitted by Unknown Agents

Many raspberry virus diseases qualify for this category, but three that have been named deserve special mention.

Bushy dwarf disease: Between 1930 and 1945 Lloyd George was pre-eminent among raspberry varieties because of its productiveness, and accounted for a large proportion of the Scottish raspberry acreage. Latterly, however, commercial stocks became worthless through virus infection, and yields in eastern Scotland gradually fell from 4 or more tons per acre to an average of 25-30 cwt. By 1945 most plantations were predominantly of plants that produced short canes, more prone to autumn-fruiting than is usual in Lloyd George and with leaves that were down-curled and greasy-looking. Plants of this kind were usually infected with a mixture of viruses, but invariably contained one which caused severe blotching and necrosis in

St. Walfried raspberry (Cadman, 1952*d*). This component was also present in Lloyd George plants from England affected by a disease named bushy dwarf by Prentice (in lit.) (Cadman and Harris, 1951). It caused symptoms resembling curly dwarf (see below) in Baumforth's Seedling B but was carried without symptoms by Norfolk Giant. Most other commercial raspberry varieties seemed immune from infection by grafting and were not found infected in the field.

Healthy clones of Lloyd George have been re-introduced to commerce over the past ten years, but plantations in many parts of England and Scotland are again affected by bushy dwarf disease. Affected plants from recent outbreaks, as well as plants collected in eastern Scotland and England and kept since 1944 and 1945, all contained a virus which was readily transmitted by mechanical inoculation of sap from raspberry to herbaceous plants. This virus produces green local lesions and systemic oak-leaf and ring patterns in *Chenopodium amaranticolor* and *C. quinoa*, large green lesions and evanescent leaf mottling in cucumber (*Cucumis sativus* L.) and chlorotic or necrotic rings in inoculated White Burley tobacco (*Nicotiana tabacum* L.) leaves in winter; and it infects systemically but produces no symptoms in *N. clevelandii* Gray. It seems not to infect French bean (*Phaseolus vulgaris* L., var. The Prince) or *Petunia hybrida* Vilm. Sap from systemically infected *C. amaranticolor* leaves seems more infective in winter than in summer, but it loses infectivity when diluted more than 1/200, when heated for 10 min. at temperatures above 56° C, when stored at −10° C or when kept for more than two days at 20° C. Crude preparations from infected *N. clevelandii* and *C. quinoa* leaves examined in the electron microscope contained large spherical particles of 80-100 mμ diameter, somewhat resembling those of tomato spotted wilt virus (Black, 1955). Viruses with similar properties have been isolated from almond (*Prunus amygdalus* L.) and plum (*P. domestica* L.) in Scotland, from cherry sent from Kent by Dr. A. F. Posnette, showing necrotic line pattern symptoms, and from Red Radboud raspberry in the Netherlands (Cadman and van der Meer, unpublished).

None of these virus isolates has been transmitted from herbaceous plants to raspberry or other rosaceous hosts. Although it seems likely that they are strains of one virus and that this produces bushy dwarf disease in Lloyd George, this is not established. In raspberry, the virus is not transmitted by *A. rubi* or *A. idaei* and is not soil-borne, but seems to spread fairly rapidly. Its host range and resemblances to tomato spotted wilt virus suggest *Thrips* spp. as possible vectors.

Curly Dwarf disease: Prentice and Harris (1950) found that certain samples of poorly-growing Lloyd George plants contained virus that produced symptoms in Baumforth's Seedling B resembling those of North American leaf curl. They named the disease curly dwarf because infected plants produced numerous very weak canes with curled leaves. Infected Lloyd George plants showed no distinctive symptoms. In eastern Scotland, Norfolk Giant was commonly infected but showed no symptoms (Cadman, 1952*a*).

The symptoms in Baumforth's B closely resemble but are usually milder than those produced by bushy dwarf virus, and the two diseases may well have related causes. However, all attempts to transmit virus mechanically from infected Baumforth's B and Norfolk Giant plants have failed. Nothing is known of the mode of spread of curly dwarf disease.

Yellow blotch disease: Infection by a virulent strain of cucumber mosaic virus seems a possible explanation for the yellow blotch disease of Lloyd George in east Perthshire, described by Cadman and Harris (1952), but unfortunately their virus isolates have since been lost and no further outbreaks of the disease have been noticed in the original localities. The strain of cucumber mosaic virus isolated by Harrison (1958*d*) did not kill Lloyd George, but no tests were made to find its effect on the other raspberry varieties used by Cadman and Harris (1952). In contrast to cucumber mosaic virus, yellow blotch disease appeared to spread quite rapidly in Lloyd George at one of the Perthshire sites. Cadman and Harris (1952) claimed, but did not confirm, transmission of a virus from the diseased Lloyd George plants to healthy Lloyd George seedlings by means of *A. rubi*.

Conclusion

Two obstacles to progress in the study of some raspberry viruses—lack of virus-free raspberry plants and of means of transmitting the viruses other than by grafting or insects—have disappeared, and there is an abundance of problems awaiting investigation. The advent of virus-free raspberry stocks and the initiation of breeding programmes aiming to produce seedlings that resist virus infection accentuate the need for more knowledge of the etiology of raspberry virus diseases, of the effects of viruses on yield and of the ways in which viruses spread in raspberry. The planning and operation of plant-health schemes would benefit from epidemiological studies, for, apart from the obvious gaps in knowledge about spread of viruses in raspberry, virtually nothing is known of the role of wild and other cultivated Rubi in the spread of virus infection. Indeed, the viruses of wild and cultivated *Rubus* species other than raspberry are an untouched field. Whilst there is clearly no lack of problems that would repay investigation, progress depends on the development and use of techniques that yield objective and not subjective evidence of virus identities and relationships.

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Hort. Res., 1961. Vol. 1, pp. 62-63

A SQUASH TECHNIQUE FOR THE SMALL CHROMOSOMES OF *RUBUS* AND *RIBES*

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THE following method is placed on record, having been found to be not only very rapid but also suitable for counting root-tip chromosomes of various species and cultivars of *Rubus* and *Ribes*. These chromosomes are small, sometimes numerous in *Rubus*, and notoriously difficult to stain.

Pre-treatment

Tips of vigorously growing roots of *Rubus* are pre-treated in 0·002 M aqueous solution of oxyquinoline (Tjio and Levan, 1950) for 3-4 hours at 0-10° C. A saturated aqueous solution of para-dichlorobenzene (Meyer, 1945) has been found to be preferable for *Ribes* roots.

Fixation

The pre-treated roots are then fixed in 1 : 3 acetic-alcohol for 12-24 hours. They may be stored in 70 per cent. alcohol until required.

Hydrolysis and staining

The root-tips are then hydrolysed in N hydrochloric acid at 60° C for 30 minutes. Staining is in Feulgen solution for not less than 2 hours. After transference to a slide, the tips are squashed in carmine, with the addition of a small drop of acetic acid saturated with ferric acetate applied to the edge of the cover slip. The slide is then heated gently over a low flame, as this helps to intensify the staining of the chromosomes. If, however, the heating is not given immediately after introducing the iron, the cytoplasm will darken.

Observation

Under optimal conditions the very darkly stained chromosomes stand out against the almost unstained cytoplasm (Haskell and Tun, 1961). The

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satellites, when present, are clearly seen. A green filter should be used during examination. Slides, temporarily sealed, can be kept in the refrigerator for several days before being made permanent (Celarier, 1956).

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REVIEW

PLUMS AND CHERRIES. Ministry of Agriculture, Fisheries and Food Bulletin No. 119, 2nd Edition. (London: H.M. Stationery Office, 1961. Pp. 74. 12 plates of photographs; 2 maps. Price 6s. net.)

In the thirteen years since this bulletin was first published, fresh knowledge of the subject has accumulated and made a second edition very necessary. We can well accept the claim that in this new edition 'all sections have been brought up to date in the light of research findings and developments in practice'. The present reviewer has in fact been surprised to find how thoroughly the results of recent research have been incorporated, and the writers have had the additional advantage of longer experience with new varieties, particularly the Merton cherries and the Long Ashton plums.

Though both the number of pages and the chapter headings in the two editions are identical, much of the material has been completely re-written. The two maps, in particular, are much more detailed, showing the acreages at the Fruit Tree Census of 1957 of plums and cherries over and under seven years old in the various counties.

One can be grateful to the authors for having condensed their material as much as they have, though this does not always make for easier reading. The section on plum pruning especially will not be light reading for new growers approaching the subject for the first time, but it will repay close study.

This bulletin, in fact, is essential reading for new planters of plums and cherries, whilst those who have bearing orchards can also derive much help from it. The claim that the whole field is covered is hardly an exaggeration; where such a bulletin could not give specific advice—for every grower has his own local problems—it is suggested that help should be obtained from the N.A.A.S.

After this it is perhaps unkind to mention certain details in which a further revision could be improved.

We know only too well that people seldom agree in their judgements of fruit quality; but some of the remarks on quality call for question. Most of us, surely, would regard Early Laxton as a better quality dessert plum than Early Prolific; yet here we read of Early Laxton, 'fair dessert quality', and of Early Prolific, 'quite pleasant as dessert'. Again, Warwickshire Drooper is given as of 'fair dessert quality', and Victoria as 'good as dessert if picked almost fully ripe'. Many would say that both these judgements should be reversed.

No warning is given, by the way, that the name 'Warwickshire Drooper' is used for several different forms, all similar in tree habit but differing much in fruit quality. As far as the reviewer knows, only one form is free from the tough, sour skin which spoils most of them.

Some other questionable points may be due to inadequate proof reading. Amongst sweet cherries, Merton Premier is given as 'early mid-season, picking about the same time as Noir de Guben', yet Noir de Guben is given (more correctly) as 'late mid-season'. And on page 70 we read 'acid cherries are much more akin to pears than to sweet cherries in their soil requirements'. Surely this should read 'plums', not 'pears'?

These, however, are small imperfections which hardly detract from a most interesting and highly useful bulletin.

N. H. GRUBB

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CONTENTS

Page

Foreword 1

Editorial 2

Studies on the Cultivation of Raspberries. I. Effects of planting distances and of the winter tipping of canes, by C. A. Wood, M. M. Anderson and G. H. Freeman 3

Chemical Control of Overwintered Annual Weeds in a Raspberry Plantation, by J. P. Sutherland 25

Some Factors Regulating the Use of Maleic Hydrazide for Runner Control in Strawberry Plantations, by P. A. Thompson . 29

Variety Trials of Vegetables in Scotland. VIII. Spring-sown brussels sprouts, 1955-1961, by C. North, L. H. Frith and H. Taylor 37

Raspberry Viruses and Virus Diseases in Britain, by C. H. Cadman 47

Notes and Comments:

A squash technique for the small chromosomes of *Rubus* and *Ribes*, by N. N. Tun and G. Haskell . . . 62

Reviews 64

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